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Frontispiece of JOHN PECKHAM'S *Perspectiva communis* (1504): GAURICUS (Editor), Venice.

[*facing p.* 315]

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It is fitting that this, the first issue of *Vision Research*, stands as a memorial to Commander DEAN FARNSWORTH, whose tragic death on 26 December 1959 deprived this science of one of its most dynamic workers and deprived this journal of its major founding spirit.

Ce premier numéro de *Vision Research* est dédié à la mémoire du Commandant DEAN FARNSWORTH, dont la mort tragique, le 26 décembre 1959, a privé la science d'un de ses chercheurs les plus dynamiques et ce journal de son principal fondateur.

Es geziemt sich, diese erste Ausgabe der Zeitschrift *Vision Research* dem Andenken des Herrn Commander DEAN FARNSWORTH zu widmen, dessen tragischer Tod am 26 Dezember 1959 unserer Wissenschaft einen ihrer aktivsten Mitarbeiter und dem Verlag dieser Zeitschrift ihren grossen Gründergeist raubte.

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PREFACE

In recent years an increasing number of people have expressed concern over the inadequacy of scientific communication in the field of visual science. Furthermore, because the number of research workers concentrating on the visual modality is especially large, progress in this area is proceeding extremely rapidly. The lack of a special journal in this field has been found to be increasingly awkward.

Vision Research is therefore planned directly to fill this gap.

However, it is not intended to encourage the isolation of the eye from the other senses, neither in its physical and chemical aspects, nor in its physiological and psychological ones. Nor does its specialization imply a contrived segregation of the senses in general from the remainder of the organism, or of its science from other areas of human knowledge. Such implications, we hope, will be explicitly avoided by the consistent representation, among the articles published, of the basic concept of the unity of the organic being. Nevertheless, within this framework, the present journal does reflect a concrete orientation prevalent today among a great many scholars and scientists throughout the world.

Primarily, it is hoped that workers will find significantly wider circulation for their ideas through this journal than they have been able to find in the past; while others may discover here, in one place, an increasing proportion of this genre of important papers which have previously been so widely scattered in the literature.

Efficient international communication and increased journal space are not virtues in themselves, however. They are to be welcomed, rather, as any other scientific aid, to the extent that creative and careful scholars use them well.

PREFACE

Ces dernières années ont vu croître le nombre de gens qui s'accordent a trouver insuffisants les échanges d'information scientifique dans la science visuelle. Comme en outre le nombre des travailleurs qui se consacrent à la vision est spécialement important, ce champ de recherches progresse extrêmement vite. L'absence d'un journal spécialisé dans ce domaine était de plus en plus fâcheuse.

Vision Research a pour but de combler cette lacune.

Cependant on ne se propose pas d'isoler l'oeil des autres organes sensoriels, pas plus des points de vue physique et chimique que de ceux de la physiologie et de la psychologie. La spécialisation de ce journal n'implique pas davantage une séparation entre les sens et le reste de l'organisme, ni une frontière entre son domaine scientifique et ceux des autres connaissances humaines. Nous souhaitons éviter explicitement de telles coupures en gardant constamment présent, dans les articles publiés, le concept de l'unité de l'être organique. Cependant, à l'intérieur de ce cadre, notre journal sera le reflet d'une orientation concrète qui prévaut aujourd'hui chez beaucoup d'étudiants et de chercheurs dans le monde entier.

Notre plus grand espoir est que les chercheurs puissent, grâce à ce journal, répandre leurs idées d'une façon notablement plus large que dans le passé, et d'autre part qu'on puisse trouver réunis ici des articles importants, en nombre croissant, qui se dispersaient autrefois dans des publications très variées.

Une meilleure diffusion internationale des résultats scientifiques et un accroissement de l'espace disponible pour les publications ne sont cependant pas des fins en soi; il convient plutôt de s'en féliciter, comme d'ailleurs de toute aide à la science, dans l'espoir que les étudiants sauront bien l'utiliser pour se cultiver et devenir créateurs.

VORWORT

In den letzten Jahren wurden in steigendem Masse Besorgnisse laut über mangelhaften wissenschaftlichen Gedankenaustausch auf dem Gebiet der ophthalmologischen Forschung. Da ferner die Zahl der mit der medizinischen Optik beschäftigten Forscher besonders gross ist, sind aussergewöhnlichrasche Fortschritte auf diesem Gebiet zu verzeichnen. Der Mangel an einer Spezialzeitschrift für diesen wissenschaftlichen Zweig wurde mit wachsender Empfindlichkeit spürbar.

Die Zeitschrift *Vision Research* soll daher diese Lücke unmittelbar ausfüllen.

Sie soll jedoch nicht dazu dienen, die Absonderung des menschlichen Auges von den übrigen Sinnesorganen in physischer, chemischer, physiologischer oder psychologischer Hinsicht zu fördern. Auch soll durch ihre Spezialausrichtung einer bewussten Trennung der Sinne im allgemeinen von dem übrigen Organismus oder dieser Wissenschaft von den übrigen Bereichen menschlichen Wissens kein Vorschub geleistet werden. Derartige Tendenzen hoffen wir, durch konsequente Darstellung des Grundbegriffs von der Einheit des organischen Wesens in den veröffentlichten Artikeln ausräumen zu können. Nichtsdestoweniger gibt die vorliegende Zeitschrift innerhalb dieses Rahmens eine festgelegte Ausrichtung wieder, welche heute bei zahlreichen Gelehrten und Wissenschaftlern in der ganzen Welt vorherrschend ist.

In erster Linie hoffen wir, dass unsere Mitarbeiter durch diese Zeitschrift eine bedeutend weitere Verbreitung ihrer Gedanken erfahren, als dies in der Vergangenheit möglich war. Andere wiederum mögen hier ein steigendes Mass an bedeutenden Fachbeiträgen auf diesem Gebiet gesammelt vorfinden, welche bislang nur über einen weiten Literaturbereich verstreut zu finden waren.

Ein lebhafter internationaler Gedankenaustausch und erweiterter Spaltenraum in der Presse sind jedoch an und für sich noch keine Tugenden. Sie sind vielmehr als wissenschaftliche Hilfsmittel wie jedes andere dieser Art zu begrüssen, und es ist von ihnen zu hoffen, dass schöpferische und gründliche Gelehrte sich ihrer vorteilhaft bedienen.

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LET'S LOOK AT THOSE ISOCHROMATIC LINES AGAIN

D. FARNSWORTH[1]

F. H. G. PITT published a paper on the "Characteristics of Dichromatic Vision" in 1935 which has had a continuing influence, and in many cases an unfortunate one, on the course of thinking about color blindness and the fundamental mechanisms of color sensation. This examination is less a criticism of Pitt's paper than a criticism of its uncritical acceptance and a consequent remarkable number of misleading beliefs which have resulted from its publication. The erroneous assumptions are in part the fault of the somewhat misleading presentation of the data by averages but many misconceptions could have been avoided if readers had been more careful to examine his method and less prone to embrace his enticingly simple diagrams as the complete statement of results.

Pitt failed to state the assumptions underlying his treatment and these implicit assumptions, plus others added to it by the readers, have much confused our thinking.

It was sometime before 1935 that Pitt had some dichromats make matches of various spectral blue–green wavelengths to mixtures of red and blue spectral lights. The question was "what to do with them?" Well, his procedure was then to find which blue–green wavelength matched a white of 4800°K (Illuminant "B") for each observer, *average* the figures for deuteranopic and for protanopic observers to obtain a single wavelength for each type, draw a straight line through this wavelength and the white point on the WDW diagram till it intersected the red–blue mixture locus, and thus determine a ratio by which to weight the red–blue mixtures.

The final outcome was a couple of neat diagrams, so orderly looking as to inspire unquestioned confidence in their integrity. When the isocolor lines were extended they intersected within a rather small area. This really looked like the *word*. Several people seized on

---

[1] Editor's note: This paper is, in substance, the content of a colloquium held on 11 March 1958 at the Technical Optics Section of the Imperial College, London, entitled: "Eight errors or confusion in colorimetry". Though Commander Farnsworth continued to be active in color vision research to his very last days, being concerned particularly with the concept of the uniform chromaticity scale diagram and the role of observation time on color-matching experiments, the present paper is perhaps one of his last relatively completed efforts in this field. Actually, his very last scientific work is the paper: KALMUS, H. and FARNSWORTH, D. (1959). "Impairment and recovery of taste following irradiation of the oropharynx." *J. Laryngology and Ontology* **73**, 180–182, carried out, in the highest possible spirit of scientific dedication, upon himself. Of this paper, Kalmus says (personal communication—25/10/60): "I am following this matter up in other patients and I think it might prove a starting point for some very interesting research in the field of chemical perception."

In the early planning of *Vision Research*, it was very much the hope of Commander Farnsworth that the Journal would publish from time to time, papers which, though they were not rigorous in the traditional sense, were nevertheless full of ideas and stirring of controversy. A category of "Notes, Queries, and Hunches" was pretty much what he had in mind. It is in this same spirit that the present paper is being published here now. The Editors are grateful to Dr. Helen Poulsen, of the Medical Research Laboratory, U.S.N. Submarine Base, New London, Connecticut, for help with the final editing of the present paper. Permission to publish is gratefully acknowledged from Mrs. Ruth Farnsworth, and from Dr. I. Estermann, Chief Scientist, Office of Naval Research, London.

Shortly after the colloquium, the manuscript was sent by Commander Farnsworth to a few colleagues for their comments. The editors consider it particularly fortunate to be able to publish here those of Professor W. D. Wright and of Dr. F. H. G. Pitt.

these data as a foundation on which to firm up the trichromatic theory. To Judd, seeking a neat mathematical formula, the deuteranopic isochroma lines appeared to cross around x = 1·08, y = −0·08, and he therefore selected x = 1·0, y = 0·0 as the best round figure for the missing green primary. To Pitt, caught up by an ingenious geometrical model, they appeared to cross around x = 1·25, y = −0·25 (same data, same lines, same chart), and it seemed that something around x = 1·40, y = −0·40 was the best representation of their real intersection—though to Pitt this did not indicate the position of a missing primary but that the red and green sensations had merged.

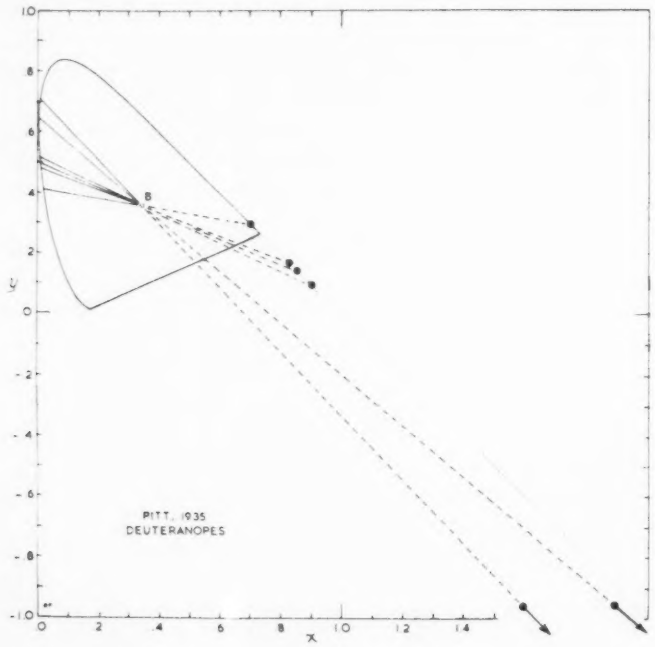

FIG. 1.

It appeared that these formulations were designed to describe something fundamental about the retinal processes irrespective of interposed filters. In Judd's words: "Pitt published data . . . in terms of the WDW coordinate system proposed by Wright for visual research because it takes account in a simple way of variations in the ocular pigmentation." And again (Hecht and Shlaer): "data may be made independent of the degree of ocular-media pigmentation by transforming them to the red and blue primaries of the WDW system. . . ." And Wright, preliminary to discussing Pitt's data: "Since the effect of differences of macular pigmentation is eliminated by the system of units employed. . . ." Whether or not these and similar statements were meant to mean that Pitt's data and results were unaffected by ocular pigmentation, they have been generally so accepted.

So we start with this widely, if not universally, accepted belief—that Pitt's study located a specific region on the mixture diagram corresponding to the missing color fundamental (by loss or fusion) of a class of dichromats and that this region was independent of the pigmentation of the observers. Now let us go back and look at Pitt's treatment.

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First of all I wanted to see how he had obtained that average figure. It would, of course, be quite justifiable if there were good agreement among the observers. But when we plot the matches of his six deuteranopes to white, the spread is hardly believable!

Protanopic and deuteranopic matches overlapping, something not obtained in any other study! But worse is to follow: the six real existing individuals with apparently impossible responses were averaged into one theoretical individual with reasonable responses. The extreme differences of the six deuteranopes which were thus hastily buried would appear to be the significant feature and the one demanding explanation. No one who is familiar with the history of visual research at the Imperial College will ascribe these differences to faulty apparatus or method. The matches are simple to make and Pitt reports them with great precision—to the fourth significant decimal in wavelength. Therefore we must accept the differences as real.

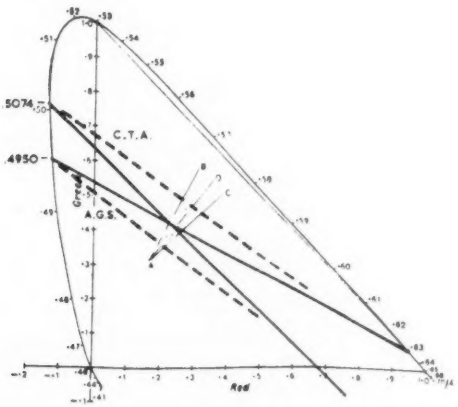

FIG. 2.

The first explanation that comes to mind is the effect of pigmentation. In fact, the range shown by Pitt's six deuteranopes is almost that of the range of Wright's thirty-six normals, and if Wright's range is due to pigmentation then there is at hand an adequate explanation of the dispersion among Pitt's observers.

Let us make a rough check of the reasonableness of this suggestion. Assuming that Pitt's observer, C.T.A., had the highest pigmentation,[2] we redraw his "isochromatic line" through the upper, or more densely pigmented, end of Wright's group of normals and the line for the extreme case (A.G.S.) through the lower, or less densely pigmented, part of his population[3] (dotted lines). The effect of this treatment is that both of these observers now exhibit similar chromaticity confusions between neutral and spectral colors. Contrary to Pitt's implication, it assumes that the excitation proportions of the fundamental receptors in dichromats are less variable than their pigmentation.

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[2] These assumptions for C.T.A. and A.G.S. are substantiated by Pitt's Table II where it is seen that the observers with the highest values for neutral points (C.T.A. and J.E.R.W.) showed a lower maximum hue-discrimination, but that those with the lowest neutral points (E.F.P. and A.G.S.) had substantially the same position of maximum hue-discrimination.

[3] Using the third case from each end to compensate for the difference in size of the populations.

It cannot be maintained that this is essentially what Pitt did in fact or in theory, by averaging his data. All we have just done is to show that the extreme differences between Pitt's observers might somewhat be reconciled by no more of an assumption than that the *range* of pigmentation in his and Wright's population was about the same. It tells us nothing of the absolute values of the pigmentation or how it would affect the effort to use color confusions to point to missing sensations.

Certainly, the belief that Pitt's method "by-passes" pigmentation is erroneous. His results literally hinge upon the match of a spectral stimulus to white light. (This largely determined the loci of intersections and his subsequent calculations were immaterial.) The hue of a spectral light is not affected by an interposed filter, the hue of a white light is most decidedly affected; thus the design of the experiment is to maximize, not eliminate, the effects of varying amounts of pigmentation. A combination of lights could scarcely be found which is more responsive to ocular pigmentation (unless it be in the Hecht–Shlaer study where a ratio of yellow–blue light is substituted for "white"). That Pitt was aware of this is shown by his statement that "The deuteranopic white point was found from the mean of six observers. On account of the variation of macular pigmentation in the eye, it would probably have been more desirable to have had more observers for this determination." Yet he disregarded the obvious implications and later writers missed the significance of it or did not agree.

Even writers who admit the pigmentation problem still act as though they expect confusion data of this sort to result in a "copunctal point" and usually on an extension of the red–green locus. This is hard to understand since pigmentation must affect color mixture in a complex way. The best we can expect is a series of crossings within a limited locus which will serve as an index of differences between observers.

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"THE AVERAGE FAMILY HAS TWO AND TWO-THIRDS CHILDREN"

A treatment which is inapplicable to individual results can scarcely be accepted as valid for application to the average of those individual results. We have spoken of the "apparently impossible response" by some of the individuals in Pitt's groups. E.F.P. and C.T.A. would provide curious samples of individuals with not one but several copunctal points, and A.G.S. is the most upsetting. His match point with white, extended, intercepts the spectral locus around 640 mμ. There is no point in belaboring the absurdity of trying to treat this case by

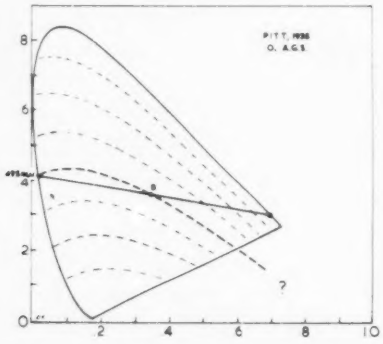

FIG. 3.

Pitt's method. The only (and it's a very simple) explanation that occurs to me is that he was wrong in his assumption—strictly untested—that confusion lines on the CIE diagram are straight lines. We can make sense of this individual's data only if we assume that his confusion line with white is curved through the two points.

The directions of the other isochroma zones would necessarily follow the trend of the light dotted lines sketched in Fig. 3, which now much resembles the diagrams calculated by VON SCHELLING (1950) representing the effect of 1 unit of a xanthophylltype filter.

These examples indicate that we cannot expect the isochromatic zones of dichromatic individuals to be straight on the CIE diagram, and it certainly removes any basic significance derived from straight line joinings and extension of averaged matched points on the diagram. It is evident that a slight disturbance of the standard color mixture functions by filtering would make the predictions from matching data extremely chancy.

"HE WENT THAT-AWAY"

The stickiest point of all concerns what we mean by this extension of lines beyond the color-mixture area to copunctal loci. No one has said exactly. If we accept the idea that the foregoing effects are due to pigmentation then it is obvious that the set of regions from which the matching chromaticities are chosen will substantially affect the results. One set cannot be as good as another (not even a representative average of any one, which might have been what Pitt and Judd subconsciously had in mind). In fact, while all contemporary authors have accepted the notion of pigmentation (the argument in this talk closely follows the general tenor of Wright's Chapter VIII), theorists in color deficiency appear to have treated the color-mixture diagram in this connexion as though it were uninfluenced by filtering effects. Until we know what colorimetric factors, and how much, to subtract from (more properly, to add to) each local area of a color-mixture diagram we don't know in what direction our isochroma lines should truly point "in the far away hills" of the fundamental color sensations.

Obviously what we need is a color-mixture diagram at the retinal level. The immediately apparent way to approach this is to devise means of measuring the quality and variety and *range* of pigmentation in normals and in color defectives.

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COMMENTS ON DEAN FARNSWORTH'S PAPER "LET'S LOOK AT THOSE ISOCHROMATIC LINES AGAIN"

F. H. G. PITT
Kodak Limited

IN DEAN FARNSWORTH'S paper "Let's look at those isochromatic lines again" he expresses doubt as to whether such lines are straight without giving any real evidence to prove that they are not. The following might clarify the point.

If a straight line is drawn in a colour triangle, such as the W.D.W. one, a colour represented as a point on this line can be made from a mixture of colours represented by points on either side of this first point. Thus if a straight line is drawn right across the colour triangle any colour represented by points along this straight line may be obtained by mixing the two colours represented by the two points formed by the intersection of this straight line with the outer "triangle". If, therefore, it is possible to plot dichromatic colours in a colour triangle, a straight line joining two colours (which to the dichromat are identical) is the loci for the mixture of identical colours and this will be an isocolour line.

The correctness of my method of producing the isocolour charts depends on two assumptions.

1. That the dichromatic system is a reduced form of the trichromatic system.
2. That the amount of macular pigmentation is the same in the average dichromatic eye as in the average trichromatic eye.

I have no doubt that the former assumption is correct. It has been reported by many observers that the dichromat always agrees with the trichromatic match and I have tested this myself to my complete satisfaction on all the dichromatic observers who made observations for me.

The second assumption cannot be proved. I have considered that if I take the average "white" point for the protanope and do the same for the deuteranope, these "white" points are representative of a protanope and deuteranope having an average amount of macular pigmentation. Farnsworth objects to this on the grounds of the dispersity of these points among the deuteranopes but states that this procedure would be justifiable if there were good agreement. Since there is in my opinion excellent agreement amongst the protanopes the range of white points being $\pm\frac{1}{2}$ colour step, I conclude that he does not object to my procedure in the case of protanopes.

I must agree that the dispersity of the white points amongst the deuteranopes is large and I would have preferred to have a much larger number of observers to have obtained the mean but having again looked at the values given in my paper I consider that these are spread reasonably uniformly over the range and I cannot believe that my average is very far out.

In *Spec. Rep. Ser. Med. Res. Coun. Lond.* No. 200, 1935, p. 48, I stated that "if one wishes to divide the colour triangle into isocolour zones for any particular deuteranope, the

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trichromatic white point and colour triangle used must represent the observations made by a trichromat having a similar macular pigmentation as the deuteranope". What Farnsworth appears to have done in Fig. 1 is to connect the white points of six deuteranopes, all having differing amounts of macular pigmentation, to a normal white point which can only represent one amount of macular pigmentation, and the resulting lines are to me meaningless—they certainly are not isocolour lines.

Summing up, I think that my deductions are still substantially correct. They are obviously not right to the "fourth significant decimal" but one often says silly things in print. This, however, although silly need not be misleading.

An interesting point posed by Farnsworth's paper is why should the dispersity of the white points of the deuteranopes in terms of colour steps be about five times that of the protanopes?

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Vision Res. Vol. 1, p. 8. Pergamon Press 1961. Printed in Great Britain.

COMMENTS AS WRITTEN TO DEAN FARNSWORTH IN 1958

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I AM sure it is a very good thing that attention should be drawn to the differences between Pitt's individual protanopes and deuteranopes and the nonsense this appears to make of his isochromatic zones. At least Pitt cannot be accused of letting his theoretical ideas influence the interpretation of his experimental data, since it was not until some years later that he realized the theoretical implications of the convergence of the protanopic zones and the near-parallelism of the deuteranopic zones.

I think in fact that his confusion loci are not so bad after all. The straightness and convergence of the dichromat's loci in the trichromat's chromaticity chart are only valid if the dichromat's colour system is a reduction system from the trichromat's. This assumption is generally based on the evidence that a dichromat will accept a trichromat's colour match, an observation which is, I believe, broadly true. However, differences of pigmentation must obviously qualify this statement, since different trichromats make different colour matches, as dichromats do also, and unless we are dealing with a trichromat and a dichromat who have the same amount of pigmentation, any attempt to represent the colour confusions of the one on the chromaticity chart of the other is mathematically invalid. Not only would the confusion loci not be straight, they would not exist at all, since stimuli with different spectral compositions but the same chromaticity for the trichromat, could have different chromaticities for the dichromat. In such a case the attempt to represent the dichromat's colour confusions on the trichromat's chromaticity chart would have no meaning.

We can now see that Pitt's analysis is only justified on the assumption that his average protanope and his average deuteranope had effectively the same pigmentation as the average trichromatic observer represented by the chromaticity chart and spectrum locus which he used. This can hardly be strictly true, but in so far as they were average observers (even if only six individuals in each case) this is likely to be a closer approximation than for any individual observer. The reasonableness of the zones themselves supports this.

One final word on the W.D.W. system and the extent to which it eliminates the effect of pigmentation. It is only the spectral chromaticity coordinates and the spectrum locus in the chromaticity chart which are unaffected in this system by pigmentation. The location of nonspectral colours in the chromaticity chart are certainly affected. In the case of tritanopia, the confusion loci could be determined from pairs of spectral stimuli (in the Thomson–Wright paper) so that in this case the convergence of the loci was independent of the pigmentation of the subjects, although the significance of the location of the co-punctal point is a function of the pigmentation of the actual observer in whose chromaticity chart the confusion loci are plotted.

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A NONLINEAR HYPOTHESIS FOR CHROMATIC ADAPTATION[1]

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Abstract—Under different ordinary qualities of illumination, a given surface retains its chromatic appearance nearly undisturbed after the observer becomes adapted to the change in quality, although the visual stimuli may be quite different for the diverse qualities. This phenomenon, called "chromatic adaptation", is customarily assumed to be equivalent to a proportional attenuation of responses that are linearly related to the physical stimuli. Analyses of data obtained recently by three independent experimenters using very different procedures indicate, however, that the hypothesis of a linear relation between the response and the stimulus fails systematically to account for the experimental results within reasonable limits of error. By combining the hypothesis of proportional attenuation and of various nonlinear relations between response and stimulus, most of the systematic errors in accounting for the experimental results can be eliminated. The most successful forms of the nonlinearities associated with the three color-receptor systems in various states of chromatic adaptation are found to be rather similar for the data of all three experiments. In general, the form of the nonlinearity thus deduced is different for each of the three color-receptor systems and, for each, is differently dependent upon the state of chromatic adaptation.

Résumé—Sous divers éclairages courants de qualité différente, une surface donnée conserve son apparence chromatique pratiquement invariable dès l'adaptation de l'observateur à l'éclairage donné, même si les stimuli visuels de ces éclairages diffèrent considérablement; de plus, l'éclairage semble rester "blanc". On assimile d'habitude ce phénomène, appelé "adaptation chromatique", à une atténuation proportionnelle des réponses des récepteurs visuels aux stimuli physiques dont ils sont une fonction linéaire. L'analyse des résultats numériques récemment obtenus par trois chercheurs indépendants et ayant employé des modes opératoires différents, indique toutefois que l'hypothèse de la relation linéaire entre les réponses et les stimuli est systématiquement erronée, même en tenant compte raisonnablement de la variance des résultats expérimentaux. Il est toutefois possible d'éliminer la plupart des erreurs systématiques dans l'interprétation des résultats expérimentaux en combinant l'hypothèse de l'atténuation proportionnelle avec diverses relations nonlinéaires entre réponse et stimulus. On a trouvé que les meilleures formes de fonctions nonlinéaires associées au système trichromatique de récepteurs dans ses divers états d'adaptation sont les mêmes pour les résultats des trois séries d'expériences. La forme de la nonlinéairité ainsi déduite est, en général, différente pour chacun des trois systèmes de récepteurs chromatiques, et en outre, pour chacun d'eux, dépend différemment de l'état d'adaptation chromatique.

Zusammenfassung—Eine gegebene Fläche behält ihr farbiges Aussehen unter verschiedenen handelsüblichen Lichtarten nahezu unverändert bei, sobald der Beobachter auf die neue Lichtart umgestimmt ist, obwohl die Sehreize für die einzelnen Lichtarten sehr verschieden sein können. Es wird gewöhnlich angenommen, dass diese "farbige Umstimmung" genannte Erscheinung mit einer proportionalen Dämpfung von Wirkungen gleichwertig ist, die mit den physikalischen Reizen linear verbunden sind. Die Auswertung von Ergebnissen, die kürzlich von drei bekannten Forschern mit sehr verschiedenen Verfahren erhalten wurden, deutet allerdings darauf hin, dass innerhalb vernünftiger Fehlergrenzen die Hypothese einer linearen Beziehung zwischen Reiz und Wirkung systematisch von den experimentellen Ergebnissen abweicht. Durch Kombina-

[1] Communication No. 2119 from the Kodak Research Laboratories, Rochester, New York.

tion der Hypothese einer proportionalen Dämpfung mit verschiedenen nicht linearen Beziehungen zwischen Reiz und Wirkung können die meisten systematischen Fehler hinsichtlich der experimentellen Ergebnisse ausgeschaltet werden. Man findet, dass für verschiedene Zustände der Farbumstimmung die erfolgreichste Form der nichtlinearen Verknüpfung der drei Farbempfängersysteme für alle drei Experimente sehr ähnlich ausfällt. Im allgemeinen ist die so abgeleitete Form der Nichtlinearität für jedes der drei Farbempfängersysteme verschieden und jedes Farbempfängersystem hängt für sich vom Zustand der Farbbestimmung ab.

* * *

There will be no difficulty in seeing how and by what mixtures the colors are made. . . . He, however, who should attempt to verify all this by experiment would forget the difference of the human and the divine nature. For God only has the knowledge and also the power which are able to combine many things into one and again resolve the one into many. But no man either is or ever will be able to accomplish either the one or the other operation.

(Plato, *Timæus 68*, Jowett translation)

NUMEROUS pairs of colors that appear identical when the observer's eyes are adapted to two different colors have been reported previously (MACADAM, 1956). Analysis has indicated that the hypothesis of a linear relation between response and stimulus (modeled after von Kries's "coefficient law") might account for those experimental results if it were assumed that color vision is mediated by five independently adapting retinal processes, each having a spectral sensitivity not expressible as a linear combination of the spectral sensitivities of the other four processes (MACADAM, 1956).

But such an assumption has a questionable corollary to the effect that some metameric color matches (i.e. matches of spectrally different stimuli) should be rendered mismatched by changes of chromatic adaptation (WYSZECKI, 1954; PARSONS, 1924; HUNT, 1952; WRIGHT, 1934, 1949). That corollary, coupled with assertions of the invariance of metameric matches or the "constancy of color match", has usually been used to "prove" that the spectral sensitivities of the processes which mediate color vision in any individual human observer must be expressible as linear combinations of not more than three wavelength-dependent functions.

The literature of color vision contains very few reports of tests of the invariance of metameric matches, and those few are surprisingly unconvincing and even contradictory. Thus, PARSONS (1924) wrote: "The law . . . is at best an incomplete statement of the facts." A recent report by DIMMICK and WIENKE (1958) indicates a serious breakdown of metameric color matches even when the changes of adaptation are quite moderate. A very recent study by WRIGHT and WYSZECKI (1960) of a suspected failure of Grassmann's laws concludes with the suggestion "that there exists a slightly photosensitive ocular pigment which, when exposed to light, changes its spectral transmittance mainly in the short and middle region of the spectrum". This, although not exactly equivalent to the suggestion of a fourth adapting process, would disturb metameric matches in much the same way and might account for the observed systematic failures of von Kries's linear-coefficient hypothesis. This possibility has not been explored.

However, in the face of the weight of authoritative opinion in support of the invariance of metameric matches, and pending the confirmation or equally authoritative acceptance of the breakdown of metameric matches indicated by Dimmick and Wienke, it seemed advisable to test alternative hypotheses that, without implying the breakdown of metameric matches for the different chromatic adaptations used, might account for the corresponding colors that are observed.

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A. HYPOTHESIS

> The law of proportion according to which the several colors are formed, even if a man knew he would be foolish in telling, for he could not give any necessary reason, nor indeed any tolerable or probable explanation of them.
>
> (Plato, *Timæus 68*, Jowett translation)

The hypothesis that is the subject of the present paper was first suggested (MACADAM, 1958) in connection with a mathematical model designed to account for the curvature of the loci of constant hue and the oval loci of constant saturation in the CIE chromaticity diagram. The hypothesis is that, for any pair of adaptations, the respective color responses (1) are nonlinearly related to the tristimulus values for properly chosen primaries and (2) bear constant ratios for all pairs of perceptually equal (called "corresponding") colors. The generalization of the hypothesis, the assumption that (3) the forms of the nonlinear relations just described are dependent on adaptation has been suggested by HUNT (1958) to account for the data of chromatic adaptation without casting doubt on the invariance of metameric matches. The specific form of nonlinear relation to be studied particularly is the power law.[2]

The simple power law

$$R = bS^p,$$

where R is the response caused by the stimulus S and b and p are constants, has a long history in psychophysics and is thus attractive for representing a nonlinear hypothesis. For example, PLATEAU (1873) originally used a simple cube-root formula to represent his brightness-scale data. Munsell's first value scale was based on the simple square-root formula (PRIEST, 1919; TYLER, 1940; GIBSON, 1940). HUNT (1957) has given a physiological argument in favor of the cube-root formula. STEVENS (1957, a and b; 1958) has surveyed many fields of psychophysics, e.g. acoustics and kinesthetics, as well as photometry, and concludes that a simple power law fits the data in each case. He reports that an exponent of about 1/3 seems suitable for brightness scales.

This type of function has been used to derive various chromaticity diagrams from the CIE tristimulus values X, Y, and Z. The so-called "chromatic value" diagram was plotted by ADAMS (1942) from tabulated values of the Munsell Value function. Some years later, TAGUTI and SATO (1956) assumed the equation

$$V = a + bY^p,$$

where V plays the role of Adams' Chromatic Value and Y may be any one of the CIE tristimulus values (X, Y, or Z) expressed as a decimal ($0{\cdot}0121 < Y < 0{\cdot}79$). They set $a=0$ and took the exponent p to be a function of Y alone when Y stands for the second CIE tristimulus value Y. When Y in the equation represents either of the other two tristimulus values, X or Z, Taguti and Sato defined p by different functions of Munsell Hue and Chroma as well as the second tristimulus value Y. The simple formula $V=bY^{1/3}$ was applied by GLASSER and his associates (1958) to produce a convenient and useful chromaticity diagram. DEKLEINE (1958) gave physiological arguments in favor of a similar use of the formula $V=bY^{1/2}$, but he also set the exponent $p=1/3$ for the second tristimulus value Y.

A comparison of the chromaticity spacing in the diagrams produced by Adams, Glasser and DeKleine was made by SUGIYAMA and FUKUDA (1959). Some of the formulas have been compared by LADD and PINNEY (1955) in terms of the root-mean-square (r.m.s.) error

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[2] Although a logarithmic law was also examined in the first test to be described, it was not examined in the other two tests, and the simple term "nonlinear hypothesis" will refer to the power law unless otherwise qualified.

of the computed V compared with the Munsell Value ($1<V<9$) and the condition that the best possible choice of a and b should be made (a not necessarily equal to zero). They found for the linear relation ($p=1$), $\sigma_V=0{\cdot}66$, for the square-root formula ($p=1/2$), $\sigma_V=0{\cdot}17$, and for the cube-root formula ($p=1/3$), $\sigma_V=0{\cdot}029$. The best formula they found was

$$V = -1{\cdot}324 + 2{\cdot}217\,Y^{0{\cdot}352},$$

in which case $\sigma_V=0{\cdot}0184$.

Another type of formula that is often used in connection with visual phenomena is logarithmic. For the simple form

$$V = a + b \log Y,$$

Ladd and Pinney found the error in V as computed to be $\sigma_V=0{\cdot}43$. Shklover (1958) proposed a chromaticity diagram based on the formula

$$V_R = \ln(R + C)$$

and similar formulas for the B and G tristimulus values computed with a set of receptor sensitivities derived from studies of dichromasy, chromatic adaptation, and color discrimination. He considered that the constant C is the same for all the receptors and that it can be neglected at high intensities to give a simple logarithmic dependence. The statement by MacAdam (1958) that logarithmic dependence would lead to straight loci of constant hue was incorrect, as Shklover pointed out in the discussion of this reference (p. 634). A subsequent test of the type of formula used by him,

$$V = a \log (bY + c),$$

with the optimum parameters, gave $\sigma_V=0{\cdot}102$.

Since, as was indicated in the preceding section, there is doubt that the response of the eye is linearly related to the physical stimulus, it is reasonable to try these two forms of nonlinear hypothesis in comparison with the von Kries linear hypothesis. Steffen (1955–1956) some years ago used the logarithmic form in an adaptation hypothesis that is otherwise quite similar to the one to be presented here. Apparently, however, the power form of the nonlinear hypothesis has never been tested.

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B. COMPUTATIONAL PROCEDURE

The equation that is the primary subject of this paper is

$$V = a + bY^p, \tag{1}$$

where V stands for any one of the postulated color responses ρ, γ, β, ρ', γ', or β' and Y stands for R, G, B, R', G', or B', respectively, in the notation of the publications of MacAdam (1956, 1958). The specific equations represented by the general equation are thus

$$\rho = a + bR^p, \text{ etc.}$$

For computational convenience, these equations were expressed by three linear equations of the type

$$V = A(0{\cdot}2857 + 1{\cdot}03\,Y^{1/2}) + (1 - A)\,(-1{\cdot}636 + 2{\cdot}468\,Y^{1/3}) \tag{1a}$$

for $0 \leq A \leq 1$

and

$$V = (A - 1)\,(2{\cdot}381 + 0{\cdot}09834\,Y) + (2 - A)\,(0{\cdot}2857 + 1{\cdot}03\,Y^{1/2}) \tag{1b}$$

for $1 \leq A \leq 2$,

which are very closely equivalent to equation (1). Here p has been replaced by A, the relation between them being as shown in Fig. 1.

The r.m.s. difference $\sigma_{1'}$ between the linear combination formulas and the power formula, equation (1), with values of the parameters that make the equations most nearly equivalent are also shown in Fig. 1. Typical curves of V vs. Y for various values of p are shown in Fig. 2.

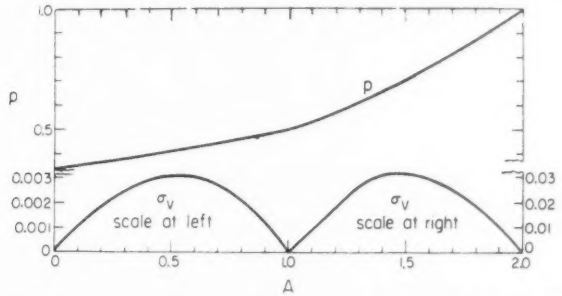

FIG. 1. Relation between exponent p in power form of nonlinear relation [Equation (1)] and parameter A in approximately equivalent equations [Equations (1a) and (1b)]. R.M.S. differences between Equation (1) and Equations (1a) and (1b) are shown by $\sigma_{1'}$.

Equations (1a) and (1b) are simply linear combinations of the most expeditiously evaluated of the formulas proposed by Ladd and Pinney. The terms containing $Y^{1/3}$ and Y are exactly the same as those proposed by Ladd and Pinney. The term in $Y^{1/2}$ was slightly changed to include the formula of this type that best fits the Munsell Value function ($\sigma_{1'} = 0{\cdot}0188$, for $A = 0{\cdot}1085$).

All the calculations on which this paper is based were performed on an IBM 705 Data Processing Machine, for which a square-root subroutine was available but for which logarithm and antilogarithm subroutines were not available when the test was begun. All the quantities were scaled so as to remain within Ladd and Pinney's ranges ($1 \leqslant V \leqslant 9$; $1{\cdot}2 < Y < 79$). Ladd and Pinney's square-root and cube-root formulas were equated to obtain a formula for a close approximation to the cube root in terms of the square-root (within the range of Y specified):

$$Z_0 = Y_0^{1/3} = 0{\cdot}799 + 0{\cdot}4233\,Y^{1/2}.$$

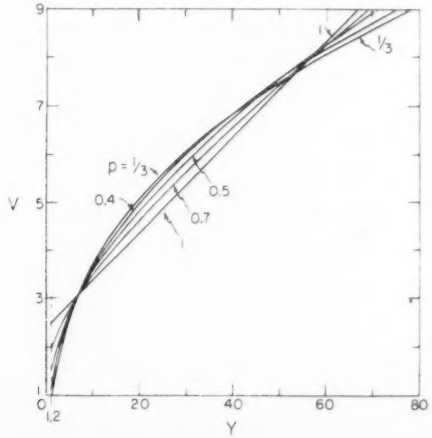

FIG. 2. Relation between V and Y in Equation (1) for values of p marked on the curves. Values of a and b were selected to reduce $\sigma_{1'}$ to a minimum for each value of p.

A sufficiently exact approximation for the cube root was then obtained by a single application of an iteration formula devised by Herzberger (1957).

$$\alpha = \frac{Y - Z_0^3}{3Z_0^2}$$

$$Y^{1/3} = Z_0 + \alpha[1 - (\alpha/Z_0)].$$

The inverse solution for Y from V (e.g. after multiplication of a corresponding value of V by an adaptation coefficient) involved the solution of a cubic equation (for $Y^{1/6}$, the cube of which was squared to obtain Y) or of a quadratic (for $Y^{1/2}$, which was squared to obtain Y). The cubic equation was solved by iteration of a simple series of operations based on the procedure given by Herzberger. The first approximation for $Y^{1/6}$, required for use in that formula, was obtained by taking the square root of the value of $Y^{1/3}$ obtained by transposing Ladd and Pinney's formula $Y^{1/3}=(V+1{\cdot}636)/2{\cdot}468$. The iteration was continued until the difference $|V(Y_n{}^{1/6})-V|$ became less than 0·0001. Usually two or three iterations were sufficient. The customary formula was used to solve the quadratic equation. These procedures were much more rapid than the use of the formula $a+bY^p$ with the logarithm and antilogarithm subroutines, which have become available since the program was devised.

C. CHOICE OF PRIMARIES

Data from Tables I to V (MacAdam, 1956) were used to compute tristimulus values R, G, B, R', G' and B' based on the Judd P and T primaries (1952) and the green primary at $x=1{\cdot}75$, $y=-0{\cdot}75$ obtained by MacAdam (1956).

A study of the detailed results, using both the linear and the nonlinear hypotheses, indicated that a few of the data were inconsistent with the remainder. Re-examination of the experimental records and the calculations of the published CIE data revealed some errors.

The following corrections were made to the work of MacAdam (1956):

Table	Obs.	Line	Corrections		
			X'	Y'	Z'
I	DLM	19	27·9	14·1	105·4
I	DLM	23	32·8	14·2	73·9
I	DLM	24	69·2	25·7	108·7
IV	EJB	3		15·2	
IV	EJB	8	121·1	100·5	
IV	EJB	10			17·5
V	EJB	last	77·4	72·1	14·7

The experimental data for the eighth and ninth pairs of corresponding colors for EJB in Table I and the sixth pair for EJB in Table III of the reference are so inconsistent with the immediately preceding and following results by the same observer, and with the corresponding results of the other observer, that they have been discarded. The inconsistencies in question are many times the spread of the repeated settings by the observer. They probably arose from a misunderstanding of the specification of the color to be matched or from a mistake in adjusting the instrument for it.

The suitability of the method of determining corresponding colors that was used to obtain the data given by MacAdam (1956) and used in the present article has been questioned by Wassef (1958) on two grounds. The first, that "the adaptation of one part of the retina to an illuminant may influence the colour perception of the part of the retina which is adapted to the other illuminant" is a possibility that was taken into account in the work reported by MacAdam (1956) and similarly in the present paper. It has not been assumed that the respective parts of the eyes are completely adapted to either adapting color, but instead the adaptation coefficients relating each group of observations for a given observer and pair of adaptations were determined from the observed data so as best to predict the corresponding colors.

It may be noted that equivalent questions can be raised concerning all other techniques for determining corresponding colors. For instance, in the binocular matching technique used by Wassef, the illuminant to which the right eye is adapted may influence the appearance of colors viewed with the left eye, even though the latter is adapted to a different illuminant. Wassef's least-squares method of determining the transformation

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matrix, which is equivalent to that originally suggested by BREWER (1954), may compensate to some extent for incomplete adaptation,[3] but it may be less effective in compensating for incomplete adaptation than the method used by MACADAM (1956) and in the present paper, because the least-squares fitting also carries the burden of compensating for all other sources of deviation from the von Kries linear hypothesis.

If, as seems to be indicated by her second criticism of the local-adaptation technique, Wassef's test and comparison samples were in view uninterruptedly for the time required to select or estimate the corresponding color, then local adaptation, which is powerful and rapid, may have rendered the adaptations of the portions of the retina with which her samples were viewed intermediate between that characteristic of the illuminant and surround and those characteristic of the various samples. When samples are fixated for more than a very few seconds, the eyes cannot be in the same state of adaptation from sample to sample. The use of the least-squares method under these circumstances would at best only determine the averages of adaptation coefficients that vary considerably from one pair of corresponding colors to another.

Wassef's second criticism of the local-adaptation technique reported by MACADAM (1956) is directed at the only method thus far suggested for avoiding such interference of the sample color with adaptation. Her criticism that the "technique in which the test and matching fields and the adapting fields were viewed alternatively . . . is not quite the natural way of seeing colours, as colours are usually seen against their adapting background" seems to overlook the fact that almost complete adaptation was maintained during each one-second exposure of the test and matching colors, so that even immediately subsequent to their removal "the artificial daylight in the left half of the field and the tungsten light in the right half of the field continued to appear almost matched".

If alternate viewing of the adapting and matching colors "is not quite the natural way of seeing colours", it is at least the only way yet suggested for maintaining the adaptations undisturbed by the test and matching colors. This idea seems to have been first used by HUNT (1952) and has since been used by others (BURNHAM, 1957). The von Kries hypothesis can be expected to be confirmed only if, in some such manner, the adaptations are maintained as nearly as possible undisturbed while all pairs of corresponding colors are determined. A merely surrounding field cannot adequately maintain adaptation during the attentive comparison of colors.

These considerations, and the fact that a greater variety of adaptations were included, support the conclusion that MacAdam's data, as corrected, are the most suitable of all available data for testing the von Kries hypothesis and for exploring alternative hypotheses.

Table 1 lists the r.m.s. errors, σ_{rk}, of prediction of the tristimulus sums resulting from the use of the von Kries linear hypothesis with six assumed locations of the green primary. The first ten rows show the results for the indicated pairs of adaptations for each observer. Adaptation A refers to tungsten light and C to artificial daylight (approximately equivalent to CIE illuminants A and C, respectively). Adaptations GY, R, B, G, and P refer to the greenish-yellow, red, blue, green, and pink adaptations specified by MACADAM (1956).

The results listed in the table are also represented in Fig. 3 by the curves numbered to correspond to the rows in Table 1. The reciprocal of x_g instead of x_g itself is plotted so that the results for $x_g = \infty$ can be included. The results in each row of the table were divided by the minimum value in that row and the relative errors thus evaluated were averaged to give the mean relative errors. These are shown in the last row of the table and by the top curve of Fig. 3.

Column 1 in Table 1 is for a green primary recently suggested by Judd in a personal communication. Column 2 is for Judd's *D*-primary (which was also used by SHKLOVER (1958)). Column 3 is for the green primary which gives the minimum mean relative error. Column 4 is for the green primary obtained by MACADAM (1956). Column 5 is for the green primary used by MACADAM (1958), which is near those derived by WALTERS (1943) and WRIGHT (1947) from their adaptation studies. That primary is also near one defined by FRY (1958) as being at the intersection of an extension of the long-wavelength end of the

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[3] Although this is not explicitly a purpose of the least-squares method, it is evident, from both equations (6) and (8) (BREWER, 1954) and the results reported there, that the best-fitting adaptation coefficients are implicit in the least-squares analysis.

BREWER (1954) found the values 1·02, 1·21 and 1·86, whereas the adaptation constants for complete adaptation to illuminants A and C reported by BURNHAM (1957) would be 1·01, 1·21 and 1·81, respectively.

TABLE 1. R.M.S. ERRORS OF PREDICTION OF TRISTIMULUS SUMS FOR LINEAR HYPOTHESIS

Data from MACADAM (1956). Each column gives the error σ_{vk} for the primaries indicated by the values of x_g, y_g for the green primary at the head.

			1	2	3	4	5	6
		Primary $x_g =$	0·66	1·00	1·40	1·75	6·85	∞
		Primary $y_g =$	0·00	0·00	−0·40	−0·75	−5·85	−∞
Line	Adaptation	Obs.						
1	A vs. C	DLM	29·20	30·38	28·58	28·47	28·26	28·12
2		EJB	20·10	9·19	7·05	6·91	6·96	7·02
3	GY vs. C	DLM	13·44	16·27	14·71	14·49	14·27	14·15
4		EJB	12·87	11·92	11·39	11·45	11·40	11·30
5	R vs. C	DLM	31·25	32·63	33·60	34·36	34·80	34·66
6		EJB	40·16	13·13	11·89	11·94	11·94	11·83
7	B vs. C	DLM	21·62	10·84	12·13	13·07	15·24	15·81
8		EJB	14·08	11·45	10·98	11·19	11·88	12·01
9	G vs. P	DLM	29·89	14·29	10·78	10·14	10·17	10·52
10		EJB	17·83	14·92	13·16	13·24	14·21	14·62
	$\langle\sigma/\sigma_{min}\rangle_{Av}$		1·805	1·142	1·041	1·044	1·079	1·088

spectrum locus and the tangent to the spectrum locus from 435 to 455 mμ. Such a primary would also be necessary to satisfy SÉGAL's (1953) specification that the sensitivity of the red receptors should be substantially zero for wavelengths shorter than 480 mμ. Column 6 is for a green primary at infinity on the straight-line extension of the long-wavelength end of the spectrum locus in the CIE chromaticity diagram.

The green primary at $x=1{\cdot}75$, $y=-0{\cdot}75$, for which results are shown in column 4, is very close to that reported by NUBERG and YUSTOVA (1958) as indicated by their studies of deuteranopia. Except where otherwise specified, it was used in all the work reported here. The green primary used by STEFFEN (1959) was at $x=1{\cdot}21$, $y=-0{\cdot}21$.

D. FIRST TEST OF HYPOTHESIS

Adaptation coefficients were computed as the weighted means of ρ'/ρ, γ'/γ and β'/β, the ratio for each pair of corresponding colors being weighted by ρ, γ and β respectively, to prevent ratios of insignificantly small responses from having undue influence on the results. This weighting was taken into account in computing the standard estimates of error, σ_1, σ_2 and σ_3, of the adaptation coefficients.

Values of ρ'_c, γ'_c and β'_c were predicted by multiplying the corresponding values of ρ, γ and β by the adaptation coefficients thus computed. These values were used to predict values of R'_c, G'_c and B'_c by reverse solution of the appropriate nonlinear formulas. Values of R'_c, G'_c and B'_c below 1·2 (Ladd and Pinney's lower limit) were discarded. The observed values (computed from the experimental values of X', Y', Z') were used in such cases. The effects of such substitutions were negligible, because only the smallest of the three responses to any one color was involved. The nonlinear adaptation hypothesis was applied to all responses of more than minimum magnitude.

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The values of X'_c, Y'_c and Z'_c, the discrepancies $\Delta X = X'_c - X'$, $\Delta Y = Y'_c - Y'$, $\Delta Z = Z'_c - Z'$ and $\Delta S = \Delta X + \Delta Y + \Delta Z$ and the discrepancy chromaticities $x_e = \Delta X/\Delta S$ and $y_e = \Delta Y/\Delta S$ were then computed. The r.m.s. value of ΔS, designated σ_s, and the covariance matrix for x_e and y_e were computed for each pair of adaptations and for each observer separately. From each covariance matrix, the half-length a of the major axis of the covariance ellipse of the discrepancy chromaticities was computed. The angle of inclination θ (measured

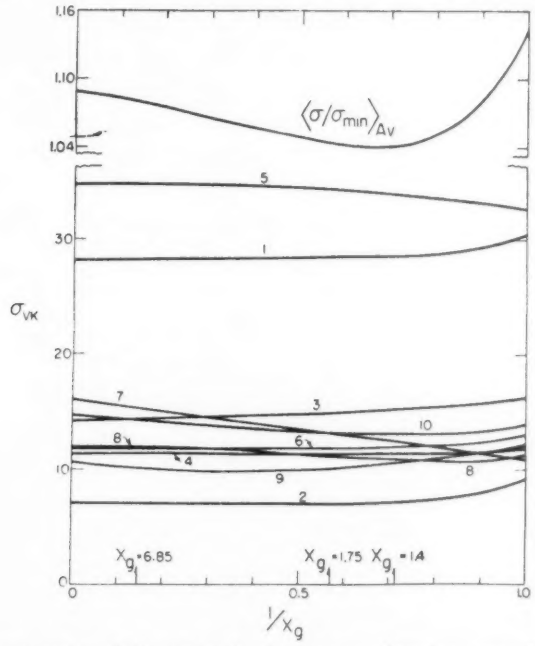

FIG. 3. R.M.S. errors of prediction of tristimulus sums resulting from use of linear (von Kries) hypothesis with MacAdam data plotted from Table 1. The numbers on the curves indicate the corresponding lines of the table.

counterclockwise from the positive horizontal axis) of the major axis and the ratio a/b of the major to the minor axis were also computed. This ratio gives the clearest indication of the degree of alignment of the discrepancy chromaticities. The smaller this ratio is (or the more nearly circular the ellipse is), the more likely it is that the discrepancies arise from random errors and not from inadequacies in the hypothesis. This ratio, therefore, indicates the magnitude of any systematic failure of prediction of the kind which suggested the earlier hypothesis of more than three adapting processes.

In the determination of the covariance matrix, each discrepancy chromaticity was weighted by ΔS^2 to prevent extremely accurate predictions (which often result in extremely high values of x_e, y_e, or both because of division by very small values of ΔS) from producing illusory indications of strong alignment.

To test the power form of the nonlinear hypothesis proposed here, the value of A in equation (1a) and (1b) between 0 and 2 for which σ_s is a minimum was determined for each of the six responses ρ, γ, β, ρ', γ', β' for each pair of adaptations and for each observer separately. The resulting values of A and the corresponding r.m.s. error of prediction σ_s are shown in Table 2. The corresponding values of the exponent p can be determined from

Fig. 1. The relative precision, within each set of six, with which each value of A was determined is indicated by the adjacent value of w. This quantity is $10^4/\sigma_s$ times an approximate value of the increase of σ_s produced by a change of 0·05 from the optimum value of A.

The values of A shown in each column in any one of the five sections of Table 2 all refer to the same adaptation condition. Thus, in the first line, A_r refers to adaptation to source A (tungsten-lamp quality) and A'_r to adaptation to source C (artificial-daylight quality) for optimum predictions of twenty-nine colors that, in daylight, would have the same appearance

TABLE 2. OPTIMUM VALUES OF PARAMETERS IN POWER FORM OF NONLINEAR HYPOTHESIS

MacAdam data. The values of A are those required to make the r.m.s. error of prediction σ_s a minimum on the assumption of a power law; w is the sensitivity to a change in A from each value listed.

Adapt.	Obs.	A_r	w_r	A'_r	w'_r	A_g	w_g	A'_g	w'_g	A_b	w_b	A'_b	w'_b	σ_s
A vs. C	DLM	0·00	12	0·91	35	2·00	0	0·00	0	1·60	20	2·00	40	22·4
Reversed	DLM	0·14	4	0·29	1	0·99	4	0·00	1	1·01	160	0·56	0	14·4
A vs. C	EJB	0·49	2	1·07	30	2·00	5	0·00	0	0·79	20	0·00	30	6·1
Reversed	EJB	0·74	2	1·25	2	2·00	12	0·00	1	0·70	10	0·00	15	7·6
GY vs. C	DLM	1·45	30	0·89	40	0·00	13	0·00	1	1·16	10	0·00	0	11·2
Reversed	DLM	1·43	20	0·84	5	0·00	13	0·00	3	0·38	0	0·00	0	12·8
GY vs. C	EJB	0·84	40	1·14	70	1·75	20	1·97	70	1·97	80	1·15	6	3·9
Reversed	EJB	0·86	70	1·16	40	1·74	2	1·72	16	1·82	70	1·14	6	4·5
R vs. C	DLM	2·00	2	0·00	2	1·43	1	1·19	50	1·44	110	2·00	50	15·0
Reversed	DLM	0·70	6	1·34	320	1·12	3	0·00	8	1·41	20	2·00	10	6·5
R vs. C	EJB	2·00	6	1·08	30	0·00	5	1·55	30	1·05	560	0·00	3	8·6
Reversed	EJB	0·65	5	1·19	20	2·00	100	0·00	20	1·55	40	1·03	1	8·9
B vs. C	DLM	0·15	1	1·29	6	2·00	100	0·00	2	1·58	11	0·57	1	9·4
Reversed	DLM	0·48	1	1·66	3	1·80	95	0·00	8	1·65	25	0·00	40	10·0
B vs. C	EJB	1·44	1450	1·92	400	1·23	15	1·11	0	2·00	46	1·88	220	5·6
Reversed	EJB	1·09	30	2·00	180	0·00	5	0·95	0	2·00	80	2·00	12	10·1
G vs. P	DLM	0·07	1	0·11	10	1·55	3	1·64	300	0·00	20	1·29	50	6·3
Reversed	DLM	0·11	14	0·09	20	2·00	20	1·58	10	0·00	7	1·72	10	4·9
G vs. P	EJB	1·02	14	1·24	10	2·00	35	0·00	1	2·00	80	2·00	40	11·6
Reversed	EJB	1·04	20	1·19	17	2·00	15	0·91	6	1·77	30	1·91	10	10·6

as twenty-nine colors actually observed in tungsten light. In the second line, labeled "Reversed", A_r refers to adaptation to source A and A'_r to source C for optimum predictions of the colors that, in tungsten light, would have the same appearance as those actually observed in daylight. Only the direction of prediction was reversed, and the unprimed and primed parameters refer to the adaptations in the order listed in the preceding line.

The values of A for the direct and the reversed directions of prediction ideally should be the same. The differences mean that a different value of the exponent p in the power law was found by the two independent computations.

The adaptation coefficients k corresponding to the values of A listed in this table are listed in Table 3. The standard estimate of error σ and the relative standard error σ/k are also given for each value of k.

To facilitate comparison, for the "reversed" cases the reciprocal $k'=1/k$ is tabulated instead of the coefficient k itself. Correspondingly, the tabulated estimate of error σ was obtained from the estimate σ itself by the formula $\sigma'=\sigma/k^2$. It may be noted that the

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relative standard errors for the direct and the reversed directions of prediction are very nearly the same when the estimates of error for the "reversed" cases are computed as just described. They should be identical; the differences arise because different laws, represented by the different values of A, were used for the two directions of prediction.

TABLE 3. ADAPTATION COEFFICIENTS FOR OPTIMUM VALUES OF PARAMETERS IN POWER FORM OF NONLINEAR HYPOTHESIS

MACADAM data. Values of k are adaptation coefficients for the corresponding values of A listed in Table 2, and σ is the standard estimate of the error in k.

Adapt.	Obs.	k_1	σ_1	σ_1/k_1	k_2	σ_2	σ_2/k_2	k_3	σ_3	σ_3/k_3
A vs. C	DLM	0·85	0·04	0·04	1·02	0·10	0·10	1·36	0·26	0·19
Reversed	DLM	0·86	0·04	0·04	0·96	0·04	0·05	1·47	0·28	0·19
A vs. C	EJB	0·87	0·05	0·06	1·10	0·14	0·12	1·48	0·14	0·10
Reversed	EJB	0·87	0·05	0·05	1·48	0·14	0·09	1·50	0·14	0·09
GY vs. C	DLM	0·94	0·07	0·07	0·95	0·05	0·05	1·57	0·07	0·05
Reversed	DLM	0·94	0·07	0·08	0·95	0·05	0·05	1·62	0·12	0·07
GY vs. C	EJB	0·95	0·03	0·03	0·95	0·05	0·06	1·24	0·10	0·08
Reversed	EJB	0·95	0·03	0·03	0·96	0·04	0·04	1·25	0·09	0·07
R vs. C	DLM	0·71	0·18	0·25	1·30	0·16	0·12	2·22	0·33	0·15
Reversed	DLM	0·66	0·03	0·04	1·38	0·24	0·18	2·27	0·32	0·14
R vs. C	EJB	0·64	0·09	0·14	1·25	0·19	0·15	3·33	0·22	0·07
Reversed	EJB	0·59	0·05	0·08	1·18	0·39	0·34	2·43	0·50	0·20
B vs. C	DLM	1·14	0·06	0·05	1·12	0·17	0·15	0·80	0·11	0·14
Reversed	DLM	1·11	0·07	0·06	1·11	0·13	0·12	0·79	0·11	0·14
B vs. C	EJB	1·04	0·08	0·08	1·00	0·04	0·04	0·84	0·14	0·17
Reversed	EJB	1·01	0·12	0·12	1·00	0·13	0·13	0·84	0·16	0·18
G vs. P	DLM	1·00	0·03	0·03	0·84	0·04	0·05	1·30	0·26	0·20
Reversed	DLM	1·00	0·03	0·03	0·86	0·04	0·05	1·30	0·28	0·22
G vs. P	EJB	0·99	0·03	0·03	0·91	0·06	0·07	1·07	0·09	0·09
Reversed	EJB	1·00	0·03	0·03	0·90	0·06	0·06	1·09	0·10	0·09

TABLE 4. ADAPTATION COEFFICIENTS FOR LINEAR (VON KRIES) HYPOTHESIS

MACADAM data. Values of k are adaptation coefficients and σ is the standard estimate of the error in k. The green primary was at $x_g = 1{\cdot}75$, $y_g = -0{\cdot}75$.

Adapt.	Obs.	k_1	σ_1	σ_1/k_1	k_2	σ_2	σ_2/k_2	k_3	σ_3	σ_3/k_3
A vs. C	DLM	0·72	0·06	0·09	0·86	0·08	0·09	2·24	1·15	0·52
	EJB	0·78	0·10	0·13	1·02	0·22	0·22	2·33	0·35	0·15
GY vs. C	DLM	0·86	0·10	0·12	0·91	0·07	0·08	2·58	0·33	0·13
	EJB	0·92	0·05	0·06	0·91	0·08	0·09	1·84	0·48	0·26
R vs. C	DLM	0·43	0·07	0·16	2·08	0·25	0·12	12·6	8·9	0·71
	EJB	0·34	0·07	0·20	1·66	0·28	0·17	15·7	3·7	0·24
B vs. C	DLM	1·46	0·15	0·10	1·16	0·08	0·07	0·54	0·30	0·56
	EJB	1·15	0·15	0·13	0·94	0·15	0·16	0·54	0·33	0·61
G vs. P	DLM	1·00	0·06	0·06	0·69	0·06	0·08	1·75	0·28	0·16
	EJB	1·01	0·06	0·06	0·70	0·06	0·09	1·29	0·37	0·29

Table 4 gives similar data for the linear hypothesis. Consideration of the weighting procedure used for calculating adaptation coefficients, stated previously, shows that the reciprocal of the adaptation coefficient for the "reversed" case must be identical with the adaptation coefficient for the "direct" case.

Although the adaptation coefficients and their standard errors shown in Table 4 are not even in principle comparable with those in Table 3, the corresponding *relative* standard errors may be compared. The average ratio of the relative errors for the linear hypothesis (Table 4) is 2·15 times that of the corresponding errors for the nonlinear hypothesis (Table 3). Moreover, out of thirty corresponding values, only four were lower for the linear hypothesis.

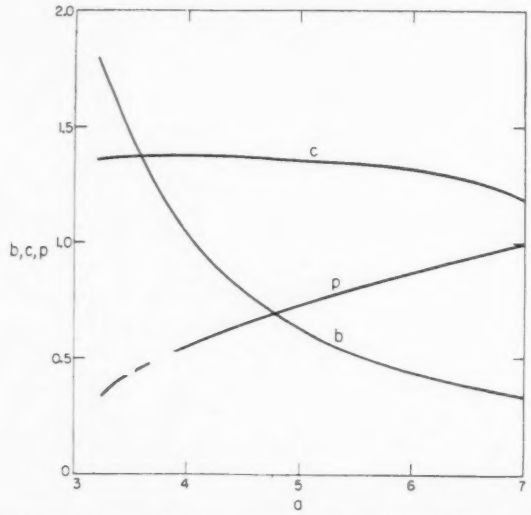

FIG. 4. Relation of b and c to the optimum value of a in logarithmic form of nonlinear relation. The curve for p represents the values of the exponent in the power form that are approximately equivalent to the optimum values of a in the logarithmic form.

The logarithmic formula $V=a \log (bY+c)$, which is as nearly as possible equivalent to that proposed by Shklover, was tested by determining the set of six optimum values of a (not listed) for each case. The corresponding adaptation coefficients, k, are listed in Table 5. The values of b and c associated with each value of a are shown in Fig. 4. They are uniquely determined by the requirements that $V=1·7$ and 7·76 for $Y=2·422$ and 54·96 respectively. The exponent p of the power formula that most nearly matches the logarithmic formula is also shown in Fig. 4 as a function of a in the logarithmic formula. It should be noted that the coefficients a and b of the power formula are quite different from a and b of the logarithmic formula.

Although the adaptation coefficients for the linear and the logarithmic forms of nonlinear hypothesis are not directly comparable, their relative standard errors can properly be compared as before. All but one of the relative errors shown in Table 4 for the linear hypothesis are greater than the corresponding errors in Table 5 for the logarithmic hypothesis, and the mean value of the errors for the linear hypothesis is 2·19 times that for the logarithmic hypothesis. The two nonlinear hypotheses are more evenly matched. In thirteen cases, the errors for the logarithmic formula are greater than the corresponding errors for the power formula (Table 3) and in twelve cases they are smaller.

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The values of p in the power formula that are approximately equivalent to the optimum values of A in Table 2 were obtained from Fig. 1 and the values that are approximately equivalent to the optimum values of a of the logarithmic (Shklover's) formula were obtained from Fig. 4. These values are listed in Table 6. This table shows that there is remarkable agreement between the two observers, as well as between the two formulas. The values which indicate the most serious disagreements between the two formulas are printed in italics. Nevertheless, including the italicized mavericks, the r.m.s. of the differences between the power law and the logarithmic form is only 0·2. The r.m.s. of the differences between the corresponding results for the two observers for both formulations is 0·33.

TABLE 5. ADAPTATION COEFFICIENTS FOR OPTIMUM VALUES OF PARAMETERS IN LOGARITHMIC (SHKLOVER) FORM OF NONLINEAR HYPOTHESIS

MACADAM data. Values of k are adaptation coefficients for optimum values of a, and σ is the standard estimate of the error in k.

Adapt.	Obs.	k_1	σ_1	σ_1/k_1	k_2	σ_2	σ_2/k_2	k_3	σ_3	σ_3/k_3
A vs. C	DLM	0·87	0·04	0·04	1·10	0·06	0·05	1·38	0·30	0·22
	EJB	0·64	0·07	0·11	1·11	0·09	0·08	3·79	0·25	0·06
GY vs. C	DLM	0·95	0·05	0·06	0·87	0·08	0·09	1·74	0·10	0·06
	EJB	0·95	0·03	0·03	0·90	0·07	0·08	1·35	0·13	0·10
R vs. C	DLM	0·67	0·07	0·10	1·24	0·07	0·06	2·77	0·61	0·22
	EJB	0·87	0·05	0·06	1·21	0·13	0·11	1·47	0·13	0·09
B vs. C	DLM	1·17	0·06	0·05	1·15	0·04	0·03	0·88	0·18	0·21
	EJB	0·98	0·07	0·07	1·09	0·07	0·06	0·84	0·22	0·26
G vs. P	DLM	0·98	0·03	0·03	0·93	0·06	0·06	1·29	0·09	0·07
	EJB	1·01	0·03	0·03	0·92	0·05	0·05	1·13	0·14	0·12

The over-all means $\langle \sigma_{vk} \rangle_{Av}$ of the relative r.m.s. errors of prediction by the linear law (Table 1), using the green primary at $x=1{\cdot}75$, $y=-0{\cdot}75$, are about 5 per cent of the corresponding tristimulus sums. The nonlinear hypothesis in either the power or the logarithmic form reduces this mean relative error about one-third. This lower error of prediction is in better accord with the experimental errors estimated by MACADAM (1956).

The chromaticities predicted according to both the linear hypothesis and the power form of the nonlinear hypothesis, using the optimum values of A, are compared in Fig. 5 with the observed chromaticities (EJB, Table V, MACADAM, 1956). The observed chromaticities are joined by dotted arrows with their respective corresponding chromaticities. The discrepancies of the nonlinear predictions from the observed chromaticities are shown by solid arrows and the discrepancies of the linear predictions by dashed arrows. Fig. 5 indicates that the nonlinear hypothesis does not give any important improvement in the accuracy of prediction for the chromaticities of corresponding colors. This lack of improvement is found to be general, for all pairs of adaptations and for all observers. But the result is otherwise with respect to predicting tristimulus sums and reducing the alignment of discrepancy chromaticities, which are the purposes for which the nonlinear hypothesis was made.

Tristimulus sums were predicted by the power law and their errors σ_s were computed. The ratios of these errors to the corresponding errors σ_{vk} for the linear hypothesis taken from column 4 of Table 8 are listed in Table 7. The means of the coordinates of the

discrepancy chromaticities, the inclination and half-length of the major axis and the ratio of the major to the minor axis of the covariance ellipse of discrepancy chromaticities for each case were computed as indicated at the beginning of this section and they are also given in Table 7. The discrepancy chromaticities and the associated covariance ellipse for the case represented in the first line of Table 7 are shown in Fig. 6. The absolute value of ΔS, the square of which was used as a weight for calculating the location, size, shape and orientation of the covariance ellipse, is written beside each point in Fig. 6. The weights are shown for both of two nearly coincident discrepancy chromaticities, at $x_e=0{\cdot}76$, $y_e=0{\cdot}24$. Coordinates and weights (very small) for two others, which fall outside the region plotted in Fig. 6, are written beside arrows pointing toward the omitted points.

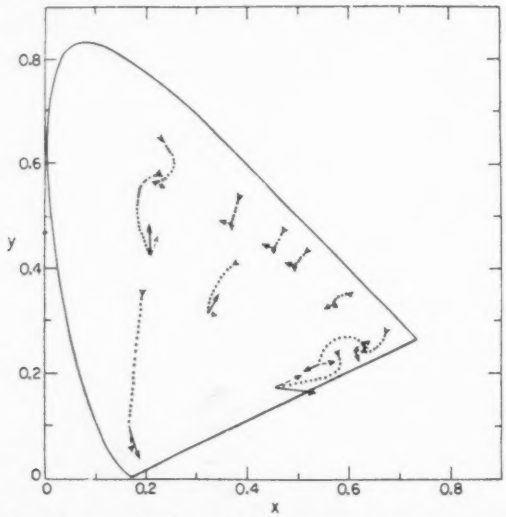

FIG. 5. Chromaticity diagram showing relation between observed chromaticities and corresponding chromaticities (dotted arrows), discrepancies according to linear hypothesis (broken arrows) and discrepancies according to power form of nonlinear hypothesis (solid arrows).

The major axes of all the covariance ellipses for which the axis ratio a/b is greater than 2·0 are shown in Fig. 7. Only axis ratios greater than 2·0 are considered to indicate a significant alignment of discrepancy chromaticities. Inclusion of the major axis for other cases ($a/b<2$) would therefore be useless as well as confusing. The number shown near each axis in Fig. 7 indicates the line in Table 7 in which the coordinates of its center, its inclination, and its half-length are given. Little or no regularity is apparent among these axis centers, lengths, or directions, even for the same observer and pairs of adaptations. Each odd and next higher even number show axes for the same observer and adaptations, with merely reversed directions of prediction. Each set, whose serial numbers end in an integral multiple of 4, is for the same pair of adaptations by both observers.

The centers of the covariance ellipses of the discrepancy chromaticities and the lengths, orientations and ratios of their axes for the linear-adaptation hypothesis are given in Table 8. The major axes for which $a/b>2$ are shown in Fig. 8, which exhibits much greater regularity than Fig. 7. The generally shorter major axes also indicate correspondingly closer adherence of the discrepancy chromaticities to those lines, even for the minimum $a/b=2{\cdot}06$. This adherence is especially close for the higher a/b ratios; for example, the first ratio in Table 8

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TABLE 6. COMPARISON OF VALUES OF p FOR NONLINEAR HYPOTHESIS

MACADAM data. For each of the tristimulus values R etc. are given the values of the exponent p corresponding to the optimum value of A for the power form (Table 2) from Fig. 1 and the value p_a corresponding to the optimum value of a in the logarithmic (Shklover) form (Fig. 4).

Adapt.	Obs.	R		R'		G		G'		B		B'	
		p	p_a	p	p_a	p	p_a	p	p_a	p	p_a	p	p_a
A vs. C	DLM	0·33	0·33	0·48	0·33	1·00	1·00	0·33	0·33	*0·74*	0·47	1·00	1·00
	EJB	0·41	0·60	0·52	1·62	1·00	1·00	0·33	0·33	0·46	0·48	0·33	0·44
	BEN	0·48		0·47		0·40		1·00		0·58		0·75	
	ETW	0·38		0·46		0·43		0·50		1·00		1·00	
GY vs. C	DLM	0·68	0·78	0·48	0·51	0·33	0·33	0·33	1·00	0·54	0·55	0·33	0·33
	EJB	0·47	0·58	0·55	0·66	*0·84*	0·33	0·98	0·80	0·98	1·00	0·55	*1·00*
G vs. C	BEN	0·47		0·49		0·48		0·99		0·59		0·49	
R vs. C	DLM	1·00	*0·48*	0·33	0·33	*0·67*	0·33	*0·56*	1·00	0·67	0·67	1·00	*1·00*
	EJB	1·00	1·00	0·52	0·33	0·33	0·33	0·72	1·00	0·52	*0·33*	0·33	0·33
B vs. C	DLM	0·36	0·47	0·60	0·64	1·00	1·00	0·33	0·64	*0·75*	1·00	0·43	0·33
	EJB	0·67	0·36	0·95	0·96	*0·58*	1·00	*0·54*	0·38	1·00	1·00	*0·92*	0·46
G vs. P	DLM	0·34	0·33	0·35	0·48	*0·73*	1·00	*0·78*	0·33	0·33	0·33	0·60	*0·33*
	EJB	0·51	0·61	0·57	0·63	1·00	1·00	0·33	0·33	1·00	1·00	1·00	1·00
G vs. A	BEN	0·47		0·49		0·40		0·77		0·44		0·48	

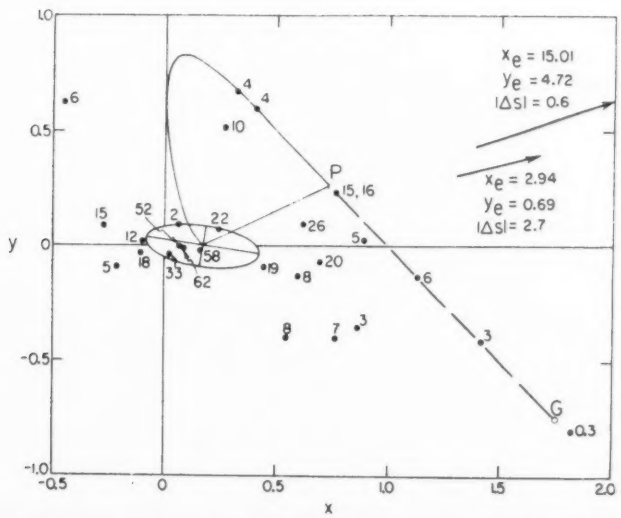

FIG. 6. Discrepancy chromaticities and covariance ellipse corresponding to line 1 of Table 7. The absolute values of ΔS are indicated for each point [two points are coincident at (0·76, 0·24)]. Two points lie outside the diagram and are indicated by arrows.

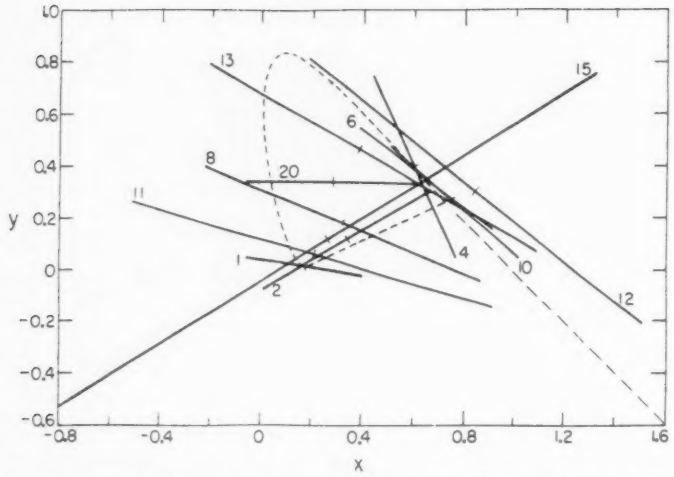

FIG. 7. Locations and lengths of major axes of discrepancy ellipses on basis of power form of nonlinear hypothesis for cases listed in Table 7 for which axis ratio exceeds 2·00. Numbers are serial numbers of lines in table.

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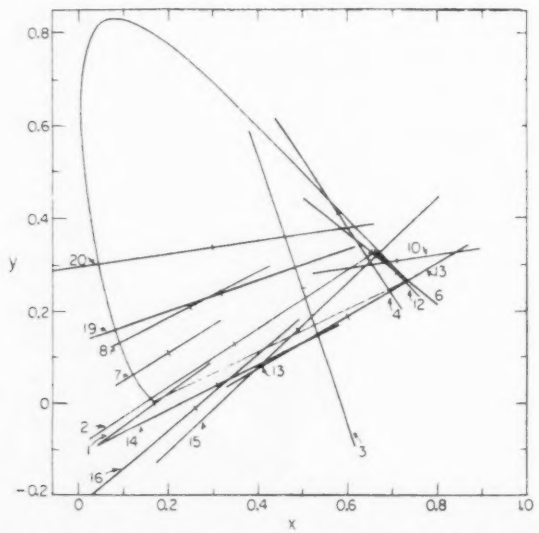

FIG. 8. Locations and lengths of major axes of discrepancy ellipses on basis of linear hypothesis for cases listed in Table 8 for which axis ratio exceeds 2·00. Numbers are serial numbers of lines in table.

is 30 per cent greater than the corresponding one in Table 7. The alignments thus indicated by Fig. 8 confirm those reported for the same data and hypothesis (MacAdam, 1956). The nonlinear hypothesis has succeeded in reducing such alignments, and therefore the systematic errors of prediction of corresponding colors, to the extent indicated by Fig. 7, in comparison with Fig. 8.

The results obtained by using the optimum constants in the logarithmic formula are shown in Table 9. The mean relative error, based on the lowest value of σ_{rk} in the corre-

sponding row of Table 1 for the linear hypothesis, is 0·73 for the optimum choices of A in the power formula and 0·84 for the optimum forms of the logarithmic formula.

Except in one instance, the corresponding values of σ_s are smaller for both types of nonlinear hypothesis than for the linear hypothesis (i.e. $\sigma_s/\sigma_{vk}<1$ in Tables 7 and 9). The superiority of the nonlinear hypotheses with respect to axis ratio, however, is less pronounced. It will be recalled that the discrepancy chromaticities which resulted from testing the linear-adaptation hypothesis were unexpectedly found to be in close alignment instead of being randomly distributed. It was to explain this phenomenon that five or more spectrally-

TABLE 7. RELATIVE ERRORS OF PREDICTION, MEAN DISCREPANCY CHROMATICITIES AND RELATED QUANTITIES FOR POWER FORM OF NONLINEAR HYPOTHESIS

MACADAM data. Relative error of prediction of tristimulus sums is σ_s/σ_{vk}, where σ_s is taken from Table 2 and σ_{vk} from Table 8; coordinates of mean discrepancy chromaticities are $\langle x_e\rangle_{Av}$ and $\langle y_e\rangle_{Av}$; inclination, half-lengths of major axes, and ratios of major to minor axis of discrepancy ellipse are θ, a and a/b, respectively.

Line	Adapt.	Obs.	σ_s/σ_{vk}	$\langle x_e\rangle_{Av}$	$\langle y_e\rangle_{Av}$	θ	a	a/b
1	A vs. C	DLM	0·79	0·17	0·01	172°	0·24	2·70
2	Reversed	DLM	0·98	0·34	0·12	30	0·38	3·54
3	A vs. C	EJB	0·88	0·51	0·35	99	0·40	1·39
4	Reversed	EJB	0·89	0·60	0·40	117	0·39	4·07
5	GY vs. C	DLM	0·77	0·60	0·36	150	0·33	1·95
6	Reversed	DLM	0·80	0·65	0·35	143	0·33	4·18
7	GY vs. C	EJB	0·34	0·21	0·06	177	0·76	1·58
8	Reversed	EJB	0·61	0·32	0·18	22	0·59	2·31
9	R vs. C	DLM	0·44	0·17	−0·02	85	0·29	1·21
10	Reversed	DLM	0·61	0·75	0·27	140	0·35	1·87
11	R vs. C	EJB	0·72	0·21	0·06	164	0·75	2·73
12	Reversed	EJB	0·63	0·84	0·30	142	0·83	3·18
13	B vs. C	DLM	0·72	0·44	0·43	151	0·74	2·38
14	Reversed	DLM	0·66	0·17	0·26	179	0·47	1·30
15	B vs. C	EJB	0·50	0·26	0·12	31	1·24	3·94
16	Reversed	EJB	0·61	0·11	0·05	56	0·65	1·47
17	G vs. P	DLM	0·63	0·38	0·23	52	0·59	1·58
18	Reversed	DLM	0·61	0·67	0·38	117	0·82	1·66
19	G vs. P	EJB	0·88	0·30	0·25	179	0·34	1·66
20	Reversed	EJB	0·96	0·28	0·34	180	0·40	2·49
	Average		0·70					

independent separately-adapting foveal receptors have been suggested (MACADAM, 1956). The nonlinear-adaptation hypothesis was proposed (HUNT, 1958; MACADAM, 1958) with the hope of eliminating this alignment. As pointed out previously, the nearer the axis ratio a/b approaches unity, the better this purpose is accomplished. The power form of the nonlinear hypothesis (Table 7) results in a smaller value of the ratio than the linear form (Table 8) in thirteen out of the twenty cases, and the logarithmic form in six out of the ten cases. The nonlinear hypotheses are thus superior in this respect in over half the cases, but some of the exceptions are rather pronounced. In two cases out of twenty, the ratios are up to 10 per cent greater for the power form than for the linear; in three cases they are between

TABLE 8. ERRORS OF PREDICTION, MEAN DISCREPANCY CHROMATICITIES AND RELATED QUANTITIES FOR LINEAR (VON KRIES) HYPOTHESIS

MacAdam data. R.M.S. errors of prediction of tristimulus sums are σ_{rk}; coordinates of mean discrepancy chromaticities are $\langle x_e \rangle_{Av}$ and $\langle y_e \rangle_{Av}$; inclinations, half-length of major axis, and ratio of major to minor axis of discrepancy ellipse are θ, a and a/b, respectively. The green primary was at $x_g = 1{\cdot}75$, $y_g = -0{\cdot}75$.

Line	Adapt.	Obs.	σ_{rk}	$\langle x_e \rangle_{Av}$	$\langle y_e \rangle_{Av}$	θ	a	a/b
1	A vs. C	DLM	28·47	0·17	0·00	36°	0·15	3·53
2	Reversed	DLM	14·60	0·34	0·13	33	0·38	4·12
3	A vs. C	EJB	6·91	0·50	0·35	109	0·36	2·06
4	Reversed	EJB	8·50	0·58	0·41	124	0·25	3·44
5	GY vs. C	DLM	14·49	0·57	0·32	173	0·22	1·89
6	Reversed	DLM	16·04	0·65	0·33	146	0·19	3·64
7	GY vs. C	EJB	11·45	0·20	0·11	31	0·14	2·38
8	Reversed	EJB	7·34	0·25	0·21	27	0·20	2·44
9	R vs. C	DLM	34·36	0·13	0·01	58	0·07	1·32
10	Reversed	DLM	10·67	0·71	0·31	8	0·19	3·49
11	R vs. C	EJB	11·94	0·26	0·05	23	0·19	1·23
12	Reversed	EJB	14·09	0·71	0·28	135	0·07	2·64
13	B vs. C	DLM	13·07	0·60	0·19	30	0·31	2·98
14	Reversed	DLM	15·11	0·32	0·04	26	0·30	3·84
15	B vs. C	EJB	11·88	0·49	0·16	43	0·43	2·57
16	Reversed	EJB	16·68	0·26	−0·01	40	0·30	2·37
17	G vs. P	DLM	10·14	0·44	0·22	51	0·28	1·66
18	Reversed	DLM	8·10	0·48	0·34	121	0·36	1·63
19	G vs. P	EJB	13·24	0·32	0·24	19	0·31	3·98
20	Reversed	EJB	11·04	0·30	0·34	8	0·36	2·96

TABLE 9. ERRORS OF PREDICTION, MEAN DISCREPANCY CHROMATICITIES AND RELATED QUANTITIES FOR LOGARITHMIC (SHKLOVER) FORM OF NONLINEAR HYPOTHESIS

MacAdam data. R.M.S. error of prediction of tristimulus sums is σ_s, relative error of prediction of tristimulus sums is σ_s/σ_{rk}, where σ_s is taken from Table 2 and σ_{rk} from Table 1, column 4; coordinates of mean discrepancy chromaticities are $\langle x_e \rangle_{Av}$ and $\langle y_e \rangle_{Av}$; inclination, half-lengths of major axes, and ratio of major to minor axis of discrepancy ellipse are θ, a and a/b, respectively.

Adapt.	Obs.	σ_s	σ_s/σ_{rk}	$\langle x_e \rangle_{Av}$	$\langle y_e \rangle_{Av}$	θ	a	a/b
A vs. C	DLM	24·9	0·87	0·16	0·00	31°	0·16	1·94
	EJB	6·2	0·90	0·48	0·35	94	0·42	1·57
GY vs. C	DLM	10·8	0·74	0·55	0·37	148	0·60	3·01
	EJB	8·1	0·71	0·18	0·15	114	0·32	1·20
R vs. C	DLM	17·0	0·50	0·12	−0·03	36	0·20	1·53
	EJB	8·2	0·69	0·11	−0·09	11	0·33	1·50
B vs. C	DLM	13·3	1·02	0·53	0·18	32	0·34	3·38
	EJB	7·3	0·65	0·25	−0·04	48	0·55	1·37
G vs. P	DLM	9·1	0·90	0·38	0·29	150	0·41	1·43
	EJB	12·9	0·98	0·35	0·23	17	0·29	1·70
Average			0·80					

TABLE 10. R.M.S. ERRORS OF PREDICTION OF TRISTIMULUS SUMS FOR LINEAR HYPOTHESIS

Data from BURNHAM *et al.* (1957). Each column gives the error σ_{vk} for the primaries indicated by the values of x_g, y_g for the green primary at the head. Tabulated values of σ_{vk} are to be multiplied by 10^{-4}. These values were determined directly from the data supplied and are not comparable with the values in Table 1 for the MacAdam data because of the difference in scale between the two sets of data.

			1	2	3	4	5	6
	Primary	$x_g =$	0·66	1·0	1·4	1·75	6·85	∞
		$y_g =$	0	0	−0·4	−0·75	−5·85	−∞
Line	Adapt.	Obs.[4]						
1	A vs. C	115	468	83	45	41	54	41
2	A vs. C	125	322	112	88	90	92	91
3	A vs. C	110	350	90	58	58	60	60
4	C vs. A	110	274	82	58	54	52	53
5	A vs. C	215	312	428	409	409	405	402
6	A vs. C	225	309	141	135	136	139	139
7	A vs. C	210	290	239	214	212	207	205
8	C vs. A	210	222	83	55	52	49	49
9	A vs. C	310	374	182	186	195	204	204
10	C vs. A	310	274	70	58	65	81	85
11	A vs. C	405	409	237	220	222	221	219
12	C vs. A	405	322	114	95	90	82	81
13	G vs. C	115	410	119	101	102	103	104
14	G vs. C	125	363	100	77	78	78	77
15	G vs. C	110	385	104	83	84	84	85
16	C vs. G	110	331	58	59	60	62	63
17	G vs. C	215	411	92	79	78	78	79
18	G vs. C	225	454	105	99	99	100	101
19	G vs. C	210	431	92	81	81	82	83
20	C vs. G	210	368	71	55	55	55	56
21	G vs. C	310	431	166	155	156	152	150
22	C vs. G	310	364	72	61	61	61	61
23	G vs. C	405	445	258	244	246	247	245
24	C vs. G	405	376	107	111	113	115	116
25	G vs. A	115	82	69	56	63	78	82
26	G vs. A	125	86	66	46	52	67	72
27	G vs. A	110	77	58	39	47	65	70
28	A vs. G	110	331	58	59	60	62	63
29	G vs. A	215	203	157	151	149	146	146
30	G vs. A	225	188	109	89	91	99	102
31	G vs. A	210	170	94	77	76	77	78
32	A vs. G	210	179	95	72	71	72	72
33	G vs. A	310	97	86	72	78	95	100
34	A vs. G	310	107	73	68	74	85	88
35	G vs. A	405	90	92	76	79	88	91
36	A vs. G	405	97	81	71	75	84	87
	$\langle \sigma/\sigma_{min} \rangle_{Av}$		3·401	1·256	1·033	1·062	1·138	1·150

[4] First digit indicates observer (1, 2, 3 or 4). Last two digits indicate group of data: 15 indicates results based on first 5 observations; 25 indicates second 5 observations; 10 indicates results of all 10 observations; 05 indicates results for the only 5 observations that were made by observer 4.

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10 per cent and 20 per cent greater; and in two cases they are more than 50 per cent greater. In three cases out of ten, the ratios are between 14 per cent and 22 per cent greater for the logarithmic form than for the linear and in one case the ratio is almost 60 per cent greater. To the extent indicated by these exceptions, the nonlinear hypotheses have failed to fulfill the purpose for which they were designed.

E. SECOND TEST OF NONLINEAR HYPOTHESIS

By using six arbitrarily adjustable parameters (the A's), as was done in the preceding section, it is not surprising that the errors for any one set of data and even systematic trends can be significantly reduced. It therefore seemed desirable to test this nonlinear hypothesis with other sets of data. This has been done by using sets of data on corresponding colors obtained by BURNHAM, EVANS and NEWHALL (1957), who used experimental arrangements and procedures quite different from those used by DLM and EJB (1956). The original tristimulus data, kindly furnished by Dr. Burnham, have been used for this test. Table 10 summarizes the results obtained with these data for the linear hypothesis in the style of Table 1 for the MacAdam data. For each adaptation condition, twelve colors were determined by each observer. As in Table 1, the mean relative errors shown in the last line indicate that a green primary on the extension of the red end of the spectrum locus between $x=1{\cdot}4$ and $1{\cdot}75$ accounts most successfully for the data. The adaptation coefficients, their standard deviations and their relative standard deviations for the linear hypothesis using the green primary at $x=1{\cdot}75$, $y=-0{\cdot}175$ are given in Table 11, which corresponds to Table 4.

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TABLE 11. ADAPTATION COEFFICIENTS FOR LINEAR (VON KRIES) HYPOTHESIS

BURNHAM data. Values of k are adaptation coefficients and σ is the standard estimate of the error in k. The green primary was at $x_g=1{\cdot}75$, $y_g=-0{\cdot}75$. For observer code, see Table 10.

Adaptation	Obs.	k_1	σ_1	σ_1/k_1	k_2	σ_2	σ_2/k_2	k_3	σ_3	σ_3/k_3
A vs. C	110	0·92	0·06	0·07	1·20	0·09	0·08	2·72	0·36	0·13
	115	0·95	0·08	0·08	1·22	0·12	0·10	2·70	0·31	0·12
	125	0·89	0·05	0·05	1·18	0·08	0·06	2·73	0·42	0·16
	210	0·91	0·05	0·06	1·18	0·05	0·04	2·66	0·73	0·26
	215	0·92	0·08	0·08	1·19	0·07	0·06	2·48	1·13	0·45
	225	0·89	0·05	0·06	1·17	0·07	0·06	2·88	0·42	0·15
	310	0·92	0·05	0·05	1·22	0·07	0·06	3·34	1·07	0·32
	405	1·00	0·11	0·11	1·28	0·12	0·09	3·04	1·70	0·56
G vs. C	110	1·02	0·08	0·08	0·99	0·09	0·09	2·40	0·31	0·13
	115	1·05	0·10	0·09	1·02	0·11	0·11	2·42	0·29	0·12
	125	1·00	0·07	0·07	0·97	0·08	0·08	2·37	0·35	0·15
	210	1·06	0·07	0·06	1·01	0·07	0·07	2·76	0·30	0·11
	215	1·00	0·09	0·09	0·98	0·09	0·09	2·84	0·36	0·13
	225	1·11	0·05	0·05	1·05	0·06	0·06	2·67	0·31	0·12
	310	1·03	0·06	0·06	0·99	0·06	0·06	2·86	0·81	0·28
	405	1·07	0·11	0·11	1·02	0·11	0·11	2·75	1·69	0·62
G vs. A	110	1·11	0·04	0·04	0·82	0·03	0·04	0·88	0·05	0·06
	115	1·10	0·07	0·06	0·83	0·05	0·06	0·90	0·07	0·08
	125	1·11	0·04	0·04	0·82	0·04	0·04	0·87	0·07	0·08
	210	1·17	0·05	0·05	0·86	0·04	0·04	1·03	0·29	0·28
	215	1·09	0·06	0·06	0·82	0·05	0·06	1·14	0·58	0·51
	225	1·25	0·07	0·06	0·90	0·06	0·06	0·93	0·08	0·08
	310	1·13	0·05	0·05	0·81	0·04	0·05	0·86	0·09	0·11
	405	1·07	0·06	0·05	0·80	0·05	0·06	0·90	0·12	0·13

TABLE 12. ADAPTATION COEFFICIENTS FOR OPTIMUM VALUES OF PARAMETERS IN POWER FORM OF NONLINEAR HYPOTHESIS

BURNHAM data. Values of k are adaptation coefficients for the corresponding values of A listed in Table 13, and σ is the standard estimate of the error in k. For observer code, see Table 10.

Adaptation	Obs.	k_1	σ_1	σ_1/k_1	k_2	σ_2	σ_2/k_2	k_3	σ_3	σ_3/k_3
A vs. C	110	0·96	0·03	0·03	1·02	0·06	0·06	1·62	0·07	0·04
Reversed	110	0·96	0·03	0·03	1·03	0·05	0·05	1·63	0·08	0·05
A vs. C	115	0·97	0·04	0·04	1·02	0·07	0·07	1·61	0·10	0·06
A vs. C	125	0·95	0·02	0·03	1·00	0·06	0·06	1·61	0·08	0·05
A vs. C	210	0·95	0·03	0·03	0·99	0·07	0·07	1·51	0·17	0·11
Reversed	210	0·95	0·03	0·03	1·00	0·06	0·06	1·61	0·20	0·13
A vs. C	215	0·92	0·05	0·06	1·01	0·06	0·06	1·49	0·23	0·15
A vs. C	225	0·96	0·03	0·03	0·99	0·07	0·08	1·65	0·11	0·07
A vs. C	310	0·99	0·03	0·03	1·02	0·05	0·05	1·73	0·12	0·07
Reversed	310	0·96	0·03	0·03	1·15	0·05	0·04	1·78	0·16	0·09
A vs. C	405	0·99	0·05	0·05	1·02	0·08	0·08	1·64	0·17	0·10
Reversed	405	0·99	0·05	0·05	1·03	0·08	0·08	1·76	0·25	0·14
G vs. C	110	1·01	0·04	0·04	0·92	0·07	0·07	1·53	0·05	0·04
Reversed	110	1·00	0·04	0·04	0·92	0·07	0·07	1·53	0·09	0·06
G vs. C	115	1·02	0·05	0·05	0·93	0·08	0·08	1·53	0·07	0·04
G vs. C	125	1·00	0·03	0·03	0·91	0·06	0·07	1·52	0·05	0·03
G vs. C	210	1·02	0·03	0·03	0·95	0·05	0·05	1·63	0·09	0·05
Reversed	210	1·02	0·03	0·03	0·94	0·06	0·06	1·62	0·17	0·10
G vs. C	215	1·00	0·04	0·04	0·93	0·06	0·06	1·65	0·11	0·07
G vs. C	225	1·06	0·03	0·03	0·97	0·05	0·05	1·60	0·08	0·05
G vs. C	310	1·04	0·03	0·03	0·92	0·05	0·06	1·62	0·12	0·07
Reversed	310	1·02	0·03	0·03	1·00	0·03	0·03	1·68	0·13	0·08
G vs. C	405	1·02	0·05	0·05	0·93	0·09	0·09	1·57	0·16	0·10
Reversed	405	1·02	0·05	0·05	0·93	0·08	0·09	1·66	0·18	0·11
G vs. A	110	1·05	0·02	0·02	0·86	0·03	0·04	0·95	0·05	0·05
Reversed	110	1·04	0·02	0·02	0·83	0·05	0·06	0·94	0·03	0·03
G vs. A	115	1·05	0·03	0·03	0·86	0·05	0·05	0·95	0·07	0·08
G vs. A	125	1·05	0·02	0·02	0·86	0·03	0·04	0·94	0·04	0·04
G vs. A	210	1·08	0·02	0·02	0·95	0·03	0·03	1·01	0·11	0·11
Reversed	210	1·07	0·02	0·02	0·92	0·02	0·02	1·00	0·14	0·14
G vs. A	215	1·06	0·03	0·03	0·85	0·05	0·06	1·04	0·20	0·19
G vs. A	225	1·11	0·03	0·03	1·04	0·07	0·07	0·97	0·05	0·05
G vs. A	310	1·05	0·02	0·02	0·84	0·05	0·06	0·93	0·05	0·05
Reversed	310	1·04	0·02	0·02	0·83	0·05	0·06	0·93	0·06	0·07
G vs. A	405	1·03	0·03	0·03	0·84	0·05	0·07	0·95	0·07	0·07
Reversed	405	1·03	0·03	0·03	0·82	0·06	0·08	0·95	0·08	0·08

Similar results for the power form of the nonlinear hypothesis, the same green primary, and optimized values of A are shown in Table 12, which corresponds to Table 3. The values for the reversed directions of prediction are tabulated in the same manner as in Table 3. The optimized values of A and their sensitivities to change are shown in Table 13 in the same manner as in Table 2. The means, weighted by w for each pair of adaptations, together with their weighted standard deviations and mean weights, are also shown in Table 13. The values of the exponent p corresponding to the weighted means of the values of A have been determined from Fig. 1 and listed in the table. These values are also shown in Table 6, in the line labeled BEN.

The r.m.s. errors of prediction σ_s of the tristimulus sums for the nonlinear hypothesis are listed in Table 14. Their ratios to σ_{rk} (σ_{rk} from column 4 of Table 10), their mean

TABLE 13. OPTIMUM VALUES OF PARAMETERS IN POWER FORM OF NONLINEAR HYPOTHESIS

BURNHAM data. The values of A are those required to make the r.m.s. error of prediction σ_e a minimum on the assumption of a power law; w is the sensitivity to a change in A from each value listed. For observer code, see Table 10.

Adaptation	Obs.	A_r	w_r	A'_r	w'_r	A_g	w_g	A'_g	w'_g	A_b	w_b	A'_b	w'_b
A vs. C	115	0·70	35	0·95	53	0·95	13	2·00	36	0·95	131	0·82	167
A vs. C	125	0·95	18	0·88	16	0·95	5	2·00	31	1·18	100	1·16	50
A vs. C	110	0·88	29	0·95	25	0·99	4	1·82	2	1·15	323	0·85	40
Reversed	110	0·23	59	0·38	47	0·59	2	1·67	5	1·16	150	0·00	6
A vs. C	215	0·47	1	1·47	2	0·85	1	2·00	4	1·45	16	2·00	356
A vs. C	225	1·40	31	0·95	18	0·00	35	2·00	39	0·89	23	0·78	7
A vs. C	210	0·84	5	0·95	5	0·00	15	2·00	90	1·25	14	2·00	220
Reversed	210	0·95	88	0·95	62	0·81	3	2·00	31	0·95	21	1·13	14
A vs. C	310	1·53	48	0·95	25	0·95	8	2·00	42	1·30	226	2·00	111
Reversed	310	0·95	36	0·44	37	1·58	3	0·50	1	1·17	70	1·34	12
A vs. C	405	0·86	6	1·13	3	0·00	7	2·00	18	1·44	53	1·95	10
Reversed	405	0·86	10	1·08	13	0·22	1	2·00	36	1·25	25	0·68	3
$\langle A\rangle_{Av}$, $\langle w\rangle_{Av}$		0·90	31	0·81	25	0·40	8	1·99	28	1·18	96	1·59	88
(σ_A)		(0·38)		(0·21)		(0·48)		(0·09)		(0·14)		(0·62)	
p		0·48		0·47		0·40		0·35		0·56		0·76	
G vs. C	115	0·42	6	0·95	10	0·63	0	2·00	39	1·17	76	0·82	41
G vs. C	125	0·77	22	0·95	31	0·95	10	2·00	88	1·25	138	1·07	76
G vs. C	110	0·62	14	0·95	21	0·95	10	2·00	62	1·20	120	0·95	62
Reversed	110	0·59	43	1·10	61	0·44	7	2·00	189	1·04	59	0·80	9
G vs. C	215	0·86	6	0·95	17	1·09	1	1·85	0	0·95	26	0·76	15
G vs. C	225	1·14	20	0·96	23	0·00	0	0·54	0	1·06	80	0·29	6
G vs. C	210	0·95	10	0·95	27	0·75	0	1·80	1	0·95	39	0·48	18
Reversed	210	0·95	27	0·95	60	0·84	4	2·00	24	0·00	31	0·11	4
G vs. C	310	1·28	12	0·95	100	0·95	2	2·00	60	1·31	64	1·55	31
Reversed	310	1·03	11	0·82	37	0·95	3	0·95	1	1·25	34	0·95	5
G vs. C	405	0·65	1	1·14	3	0·00	7	2·00	235	1·55	27	1·85	15
Reversed	405	0·81	3	1·11	17	0·00	34	2·00	106	1·45	30	0·95	8
$\langle A\rangle_{Av}$, $\langle w\rangle_{Av}$		0·84	14	0·95	34	0·39	7	1·99	68	1·15	58	0·94	26
(σ_A)		(0·23)		(0·18)		(0·44)		(0·10)		(0·28)		(0·35)	
p		0·47		0·49		0·40		0·99		0·55		0·49	
G vs. A	115	0·75	18	0·95	30	0·00	19	1·65	2	0·95	11	0·00	26
G vs. A	125	0·76	40	0·95	51	0·00	8	1·56	3	0·74	2	0·95	16
G vs. A	110	0·76	44	0·95	70	0·00	28	1·55	4	0·95	20	0·37	3
Reversed	110	0·96	56	1·13	147	0·00	60	2·00	8	0·68	5	0·94	7
G vs. A	215	1·18	7	0·90	7	0·81	0	1·84	0	0·80	7	1·59	12
G vs. A	225	0·69	15	0·95	36	2·00	31	0·00	12	0·95	11	1·14	16
G vs. A	210	0·87	18	0·95	30	1·82	5	1·55	6	0·95	12	1·42	45
Reversed	210	0·85	6	1·04	33	0·45	1	0·95	3	0·00	43	1·39	32
G vs. A	310	0·44	18	0·94	22	0·59	0	1·90	2	0·75	2	0·95	7
Reversed	310	0·95	24	1·25	47	0·30	1	2·00	25	0·66	2	1·02	10
G vs. A	405	0·67	12	0·95	13	0·00	5	1·76	2	0·81	26	0·43	3
Reversed	405	0·95	21	1·10	32	0·00	27	2·00	24	0·95	26	0·81	33
Average		0·86	23	0·95	43	0·39	14	1·62	8	0·66	14	0·89	18
(σ_A)		(0·15)		(0·11)		(0·11)		(0·67)		(0·38)		(0·49)	
p		0·48		0·49		0·40		0·77		0·44		0·48	

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discrepancy chromaticities and the associated data are also given in a form corresponding to Table 7. The mean relative error computed on the same basis as used for the last line of Table 10 is 0·80.

The mean discrepancy chromaticities and the inclinations of the major axes of the covariance ellipses are given for six different green primaries in Table 15 on the basis of the linear hypothesis. These quantities are shown not only for the supplemented data (BURNHAM, 1957), which were used for Table 14, but also for the revised data (MACADAM, 1956). The

TABLE 14. ERRORS OF PREDICTION, MEAN DISCREPANCY CHROMATICITIES AND RELATED QUANTITIES FOR POWER FORM OF NONLINEAR HYPOTHESIS

BURNHAM data. Error of prediction of tristimulus sums σ_s; relative error is σ_s/σ_{rk}, where σ_{rk} is taken from Table 10; coordinates of mean discrepancy chromaticities are $\langle x_e \rangle_{Av}$ and $\langle y_e \rangle_{Av}$; inclination, half-length of major axis and ratio of major to minor axis of discrepancy ellipse are θ, a and a/b, respectively. For observer code, see Table 10. Values of σ_s are to be multiplied by 10^{-4}, as in Table 10.

Adapt.	Obs.	σ_s	σ_s/σ_{rk}	$\langle x_e \rangle_{Av}$	$\langle y_e \rangle_{Av}$	θ	a	a/b
A vs. C	110	49	0·85	0·30	0·29	116°	0·91	1·76
Reversed	110	42	0·78	0·65	0·44	114	1·13	2·21
A vs. C	115	39	0·95	0·15	0·10	100	1·34	1·89
A vs. C	125	76	0·84	0·22	0·25	142	0·61	2·05
A vs. C	210	139	0·66	0·09	0·01	127	0·33	1·36
Reversed	210	45	0·87	−0·35	−0·01	11	1·00	1·21
A vs. C	215	214	0·52	0·01	0·01	34	0·34	2·23
A vs. C	225	98	0·72	0·13	0·19	167	0·83	2·75
A vs. C	310	65	0·35	0·40	0·05	176	0·79	1·92
Reversed	310	46	0·71	0·43	0·29	55	0·52	1·15
A vs. C	405	165	0·74	0·19	0·25	80	0·33	1·29
Reversed	405	81	0·89	0·36	0·30	102	0·92	2·04
G vs. C	110	65	0·77	0·09	0·52	117	0·64	2·09
Reversed	110	38	0·63	−0·01	0·72	129	2·10	4·92
G vs. C	115	85	0·83	0·15	0·46	109	0·57	2·75
G vs. C	125	55	0·71	−0·01	0·63	137	0·66	1·54
G vs. C	210	75	0·92	0·24	0·08	101	0·54	1·39
Reversed	210	42	0·76	0·54	0·16	56	1·26	2·19
G vs. C	215	78	0·99	0·26	0·19	69	0·64	1·78
G vs. C	225	81	0·82	0·22	0·11	151	0·63	1·95
G vs. C	310	101	0·65	0·23	0·24	177	0·49	1·67
Reversed	310	58	0·95	0·38	0·30	60	0·49	1·78
G vs. C	405	198	0·81	0·14	0·27	92	0·25	1·41
Reversed	405	81	0·72	0·00	0·49	128	1·38	3·38
G vs. A	110	39	0·83	0·33	0·43	135	0·58	3·96
Reversed	110	32	0·53	0·29	0·43	140	1·40	6·43
G vs. A	115	53	0·84	0·37	0·43	125	0·47	1·86
G vs. A	125	45	0·87	0·34	0·41	145	0·53	2·33
G vs. A	210	65	0·86	0·21	0·11	39	0·53	2·16
Reversed	210	59	0·83	−0·02	0·02	69	0·46	1·88
G vs. A	215	137	0·92	−0·01	0·02	27	0·36	1·70
G vs. A	225	76	0·83	0·52	0·40	145	0·88	8·33
G vs. A	310	65	0·83	0·43	0·25	140	0·56	4·60
Reversed	310	59	0·80	0·26	0·34	141	0·69	5·07
G vs. A	405	71	0·90	0·28	0·36	153	0·47	2·10
Reversed	405	63	0·84	0·13	0·48	150	0·77	3·41
Average			0·79					

TABLE 15. DEPENDENCE ON PRIMARIES OF MEAN DISCREPANCY CHROMATICITIES AND RELATED QUANTITIES

Combined data. The first 46 lines are for the linear (von Kries) hypothesis. Coordinates of mean discrepancy chromaticities are $\langle x_r \rangle_{Av}$ and $\langle y_r \rangle_{Av}$, inclination of discrepancy ellipses is θ. Green primary is indicated by x_g, with $y_g = 1 - x_g$ except for first column. The last two lines are for one observer on the nonlinear hypothesis and are comparable with lines 13 and 14, respectively. For observer code, see Table 10.

Line	Adaptation	x_g = Obs.[5]	0·66 (y_g = 0) $\langle x_r \rangle$	$\langle y_r \rangle$	θ	1·00 $\langle x_r \rangle$	$\langle y_r \rangle$	θ	1·40 $\langle x_r \rangle$	$\langle y_r \rangle$	θ	1·75 $\langle x_r \rangle$	$\langle y_r \rangle$	θ	6·85 $\langle x_r \rangle$	$\langle y_r \rangle$	θ	∞ $\langle x_r \rangle$	$\langle y_r \rangle$	θ
1	A vs. C	DLM	0·24	−0·18	93°	0·23	−0·21	105°	0·17	0·01	33°	0·17	0·00	36°	0·17	0·00	34°	0·17	0·00	34°
2	A vs. C	EJB	0·17	0·16	101	0·67	−0·55	101	0·52	0·34	109	0·50	0·35	109	0·50	0·37	104	0·50	0·39	105
3	GY vs. C	DLM	0·35	−0·39	100	0·66	−0·39	103	0·57	0·32	169	0·57	0·32	173	0·56	0·32	172	0·56	0·32	172
4	GY vs. C	EJB	0·23	0·17	89	0·29	−0·03	100	0·20	0·11	26	0·20	0·11	31	0·20	0·11	32	0·20	0·10	32
5	R vs. C	DLM	0·19	−0·02	151	0·11	0·04	156	0·11	0·01	8	0·13	0·01	58	0·13	0·02	95	0·13	0·02	100
6	R vs. C	EJB	0·11	0·02	130	0·41	−0·05	130	0·27	0·04	17	0·26	0·05	23	0·24	0·06	94	0·23	0·05	97
7	B vs. C	DLM	0·25	−0·04	97	0·59	−0·61	104	0·57	0·18	32	0·60	0·19	30	0·64	0·21	32	0·65	0·21	33
8	B vs. C	EJB	0·22	0·10	89	0·57	−0·08	172	0·47	0·17	43	0·49	0·16	43	0·51	0·15	43	0·52	0·15	43
9	G vs. P	DLM	0·31	0·08	86	0·59	−0·08	95	0·47	0·21	54	0·44	0·22	51	0·50	0·20	40	0·51	0·20	36
10	G vs. P	EJB	0·42	0·28	90	0·46	−0·01	100	0·31	0·23	15	0·32	0·24	19	0·38	0·26	18	0·41	0·27	18
11	A vs. C	115	−0·13	0·20	137	0·72	−0·66	98	0·41	0·56	72	0·32	0·52	77	−0·06	0·06	165	0·36	0·43	78
12	A vs. C	125	−0·03	0·22	129	0·46	−0·34	111	0·22	0·05	75	0·23	0·30	82	0·25	0·03	76	0·26	0·03	77
13	A vs. C	110	0·01	0·21	127	0·60	−0·57	106	0·26	0·13	73	0·25	0·08	80	0·27	0·05	77	0·29	0·05	78
14	C vs. A	110	0·03	0·01	62	0·70	−0·05	143	0·53	0·59	63	0·51	0·61	72	0·54	0·55	86	0·53	0·53	88
15	A vs. C	215	−0·04	0·15	108	0·10	−0·11	119	0·05	−0·04	55	0·05	−0·04	58	0·04	−0·04	55	0·04	−0·05	55
16	A vs. C	225	−0·07	0·25	114	0·30	−0·08	108	0·20	0·16	61	0·22	0·16	57	0·23	0·18	54	0·23	0·18	53
17	A vs. C	210	−0·07	0·21	112	0·16	−0·26	119	0·05	−0·07	59	0·04	−0·07	59	0·02	−0·08	54	0·02	−0·08	54
18	C vs. A	210	−0·08	−0·14	7	0·47	−0·71	106	−0·05	0·00	37	−0·01	0·01	38	0·01	0·08	35	0·06	0·11	34
19	A vs. C	310	−0·02	0·26	113	0·17	0·03	110	0·14	−0·04	65	0·18	−0·04	61	0·19	−0·01	54	0·20	−0·01	55
20	C vs. A	310	−0·04	−0·16	64	0·71	−1·55	96	0·32	0·21	48	0·36	0·19	52	0·42	0·20	50	0·44	0·21	49
21	A vs. C	405	0·08	0·26	123	0·23	−0·19	127	0·13	−0·08	56	0·13	−0·10	62	0·12	−0·10	61	0·12	−0·11	63
22	C vs. A	405	0·11	0·06	65	0·65	0·28	93	0·53	0·40	49	0·50	0·39	52	0·46	0·36	52	0·46	0·36	52
23	G vs. C	115	0·21	0·09	92	0·44	−0·32	104	0·30	0·30	82	0·22	0·30	84	0·30	0·31	81	0·23	0·22	81
24	G vs. C	125	0·20	0·07	93	0·46	−0·45	102	0·22	0·13	77	0·22	0·13	80	0·22	0·14	76	0·23	0·15	76
25	G vs. C	110	0·21	0·08	93	0·47	−0·46	103	0·27	0·22	81	0·27	0·22	83	0·28	0·23	80	0·28	0·24	80
26	C vs. G	110	0·21	0·07	89	0·44	1·00	101	0·30	0·59	89	0·32	0·57	91	0·33	0·56	90	0·34	0·56	89
27	G vs. C	215	0·23	0·11	86	0·45	−0·11	96	0·31	0·31	61	0·30	0·31	63	0·31	0·32	60	0·32	0·32	61
28	G vs. C	225	0·24	0·14	85	0·31	−0·18	102	0·18	0·15	71	0·18	0·14	74	0·19	0·14	72	0·19	0·15	73
29	G vs. C	210	0·23	0·12	95	0·41	−0·21	100	0·26	0·23	68	0·25	0·23	70	0·26	0·23	67	0·26	0·24	68
30	C vs. G	210	0·24	0·02	86	0·59	0·03	100	0·37	0·54	73	0·36	0·55	75	0·36	0·54	71	0·37	0·54	70
31	G vs. C	310	0·22	0·09	94	0·26	0·05	108	0·16	−0·02	58	0·17	−0·03	61	0·16	−0·03	57	0·16	−0·04	57
32	C vs. G	310	0·23	−0·01	85	0·47	−0·42	88	0·31	0·23	63	0·32	0·23	65	0·33	0·23	61	0·33	0·24	59
33	G vs. C	405	0·24	0·12	91	0·24	−0·14	108	0·18	0·02	68	0·19	0·02	70	0·19	0·03	67	0·19	0·03	67
34	C vs. G	405	0·25	0·10	88	0·31	0·60	93	0·29	0·33	73	0·31	0·32	74	0·31	0·33	72	0·31	0·33	71
35	G vs. A	115	1·10	0·55	69	0·68	−1·24	96	0·43	0·38	40	0·46	0·36	41	0·51	0·35	39	0·52	0·34	37
36	G vs. A	125	1·24	0·91	81	0·72	−1·45	97	0·39	0·33	30	0·45	0·31	2	0·55	0·28	175	0·57	0·28	174
37	G vs. A	110	1·32	0·79	102	0·81	−1·98	95	0·42	0·33	153	0·49	0·31	166	0·56	0·30	166	0·57	0·30	165
38	A vs. G	110	1·31	−0·84	69	0·88	−0·92	101	0·31	0·38	158	0·44	0·31	158	0·50	0·32	161	0·52	0·31	161
39	G vs. A	215	0·31	0·29	27	0·05	0·00	110	−0·02	0·02	47	−0·02	0·02	42	−0·01	0·03	36	0·00	0·04	35
40	G vs. A	225	0·86	0·67	69	0·61	−0·54	97	0·45	0·39	125	0·45	0·39	67	0·48	0·39	2	0·49	0·38	171
41	G vs. A	210	0·69	0·56	35	0·33	−0·44	105	0·07	0·11	46	0·08	0·14	42	0·18	0·20	36	0·21	0·22	34
42	A vs. G	210	0·70	−0·43	117	0·30	−0·48	106	0·00	0·08	63	0·00	0·12	52	0·05	0·17	45	0·08	0·18	43
43	G vs. A	310	1·06	0·67	75	0·67	−0·98	99	0·47	0·27	11	0·50	0·27	13	0·56	0·27	9	0·57	0·27	8
44	A vs. G	310	1·10	−0·61	108	0·52	−0·24	101	0·37	0·29	40	0·43	0·26	3	0·49	0·28	7	0·50	0·27	7
45	G vs. A	405	0·80	0·65	66	0·57	−0·49	96	0·35	0·34	19	0·35	0·33	26	0·39	0·31	15	0·40	0·30	6
46	A vs. G	405	0·89	−0·51	114	0·52	−0·25	109	0·23	0·39	26	0·25	0·35	38	0·30	0·33	179	0·32	0·32	171
	Nonlinear hypothesis																			
47	A vs. C	110				0·49	−0·35	102	0·32	0·21	105	0·30	0·29	116	0·29	0·32	121			
48	C vs. A	110				0·88	−0·74	99	0·54	0·52	98	0·65	0·44	114	0·57	0·52	66			

[5] The numerical designations of observers indicate BURNHAM, EVANS and NEWHALL data. For code, see footnote following Table 10.

half-lengths of the major axes and the ratios of the major to the minor axes are listed in Table 16 for all the cases represented in Table 15.

Comparing the cases that are common to Tables 14 and 16, it can be seen that twenty-six of the thirty-six axis ratios for the nonlinear hypothesis (Table 14) are smaller than the corresponding ratios for the linear hypothesis (Table 16). This is better than the result found in the preceding section, where thirteen out of twenty cases were favorable to the nonlinear hypothesis. Closer examination shows that eight of the exceptions are for the G vs. A pair of adaptations. The mean value of σ_s/σ_{vk} for these is 0·9, which shows that in these cases the nonlinear hypothesis is but little better than the linear one for predicting tristimulus sums. The only other exception is with the G vs. C pair of adaptations, and here the mean value of σ_s/σ_{vk} has the lower but still comparatively high value of 0·8. For the A vs. C pair of adaptations, all the axis ratios are lower for the nonlinear predictions, which is an even better result than was found in the preceding section. The mean value of σ_s/σ_{vk} for these cases is 0·74. All but two of the A vs. C ratios for the nonlinear hypothesis are considerably less than half of those for the linear hypothesis and the average is one-third of the average ratio for the linear hypothesis.

F. THIRD TEST OF HYPOTHESIS

WASSEF (1958) determined thirty pairs of corresponding colors for adaptation to illuminants A and C. Although she specified the data for illuminant C in terms of CIE tristimulus values, she specified the corresponding colors in illuminant A only by their Munsell notations. For comparing the nonlinear with the linear hypothesis, the tristimulus values given by KELLY, GIBSON and NICKERSON (1943) have been adopted for the Munsell samples used by Wassef in illuminant A. There seems to be no alternative to this unhappy expedient.

The results obtained with Wassef's data, thus interpreted, by using the linear (von Kries) hypothesis for the same six choices of green primaries as used previously are indicated in Table 17. As in the test of the data of MACADAM (1956) and of BURNHAM (1957) (Tables 1 and 10), when $y_g=1-x_g$ the minimum r.m.s. error of prediction σ_{vk} of the tristimulus sums occurs for $1{\cdot}4 \leqslant x_g \leqslant 1{\cdot}75$. The results obtained with Wassef's data by the nonlinear hypothesis, with $x_g=1-y_g=1{\cdot}75$ and the optimum values of A, are shown in Table 18. Predicting the matches in illuminant C in this way reduces σ_s to two-thirds of the minimum value obtainable with the linear hypothesis ($\sigma_s/\sigma_{vk}=0{\cdot}66$). The ratio a/b of the major to the minor axis of the covariance ellipse for the discrepancy chromaticities is reduced from a significant 3·13 (for the same green primary, $x_g=1{\cdot}75$) to an insignificant 1·62. The nonlinear predictions of the corresponding colors in illuminant A for Wassef's data for illuminant C (the reversed case) reduce σ_s to 88 per cent of the von Kries minimum. The axis ratio a/b is correspondingly reduced from a significant 2·24 to an insignificant 1·69. The values of the exponent p, determined from Fig. 1 for the weighted means of each pair of A's in the last two columns of Table 17, are given in Table 6 in the lines for A vs. C labeled ETW. In general, the agreement with the results for the other two sets of data is good. Wassef's data, therefore, like those published by MACADAM (1956) and BURNHAM (1957), clearly indicate (1) that some modification of the von Kries linear hypothesis is needed; (2) that the nonlinear hypothesis here suggested is a definite improvement; and (3) that the adaptation-dependent forms of the most successful nonlinearities are much the same for all three sets of data.

TABLE 16. DEPENDENCE ON PRIMARIES OF LENGTHS AND RATIOS OF AXES OF DISCREPANCY ELLIPSES

Combined data. The first 46 lines are for the linear (von Kries) hypothesis. Half-length of major axis of discrepancy ellipse is a; ratio of major to minor axes is a/b. Green primary is indicated by x_g, with $y_g = 1 - x_g$ except for first column. The last two lines are for one observer on the nonlinear hypothesis and are comparable with lines 13 and 14, respectively. For observer code, see Table 10.

Line	Adapt.	x_g= Obs.	0·66 (y_g=0) a	a/b	1·00 a	a/b	1·40 a	a/b	1·75 a	a/b	6·85 a	a/b	∞ a	a/b
1	A vs. C	DLM	0·61	5·04	0·59	4·55	0·16	3·67	0·15	3·53	0·16	3·68	0·16	3·81
2	A vs. C	EJB	0·53	3·43	1·07	7·66	0·35	1·94	0·36	2·06	0·34	1·92	0·34	1·96
3	GY vs. C	DLM	1·25	2·62	1·02	7·72	0·23	1·93	0·22	1·89	0·22	1·89	0·22	1·87
4	GY vs. C	EJB	1·17	11·96	1·30	5·88	0·14	1·75	0·14	2·38	0·14	2·25	0·14	2·27
5	R vs. C	DLM	0·20	2·33	0·18	1·90	0·09	1·35	0·07	1·32	0·07	1·43	0·06	1·52
6	R vs. C	EJB	0·15	2·64	0·46	2·18	0·25	1·40	0·19	1·23	0·19	1·29	0·19	1·41
7	B vs. C	DLM	0·68	4·23	1·24	5·55	0·32	2·80	0·31	2·98	0·27	2·99	0·26	2·98
8	B vs. C	EJB	0·99	2·93	0·42	3·82	0·44	2·67	0·43	2·57	0·40	2·44	0·40	2·41
9	G vs. P	DLM	0·64	6·78	1·35	7·28	0·26	1·80	0·28	1·66	0·29	1·57	0·29	1·58
10	G vs. P	EJB	1·16	6·74	1·41	4·55	0·31	2·95	0·31	3·98	0·33	4·58	0·34	4·89
11	A vs. C	115	0·33	2·13	0·76	2·95	0·91	4·68	1·03	5·65	0·17	2·38	1·04	3·84
12	A vs. C	125	0·34	2·38	0·67	3·13	0·35	3·32	0·35	2·61	0·32	1·86	0·33	1·80
13	A vs. C	110	0·31	2·45	0·72	2·72	0·66	4·61	0·66	4·15	0·61	2·91	0·63	2·75
14	C vs. A	110	0·51	3·63	0·30	3·25	0·27	2·83	0·31	2·65	0·35	1·88	0·35	1·81
15	A vs. C	215	0·36	1·88	0·18	2·53	0·08	5·39	0·08	9·32	0·08	7·23	0·08	6·01
16	A vs. C	225	0·42	2·64	0·82	3·90	0·23	3·06	0·23	4·01	0·25	4·70	0·25	4·07
17	A vs. C	210	0·42	2·51	0·34	3·21	0·12	3·24	0·11	4·71	0·13	5·23	0·33	1·80
18	C vs. A	210	0·30	9·48	1·74	3·64	0·76	6·98	0·85	11·82	1·03	11·47	0·14	4·37
19	A vs. C	310	0·28	2·11	0·59	3·97	0·15	6·79	0·15	5·69	0·17	5·08	0·18	5·07
20	C vs. A	310	0·43	2·89	1·62	3·43	0·53	5·36	0·47	7·28	0·37	5·47	0·35	5·06
21	A vs. C	405	0·27	2·47	0·39	1·95	0·31	8·99	0·29	9·02	0·26	6·46	0·27	5·99
22	C vs. A	405	0·46	4·27	1·44	4·00	0·56	8·16	0·60	10·46	0·64	7·51	0·65	6·74
23	G vs. C	115	0·15	7·45	0·52	2·82	0·41	6·53	0·41	7·51	0·40	7·94	0·41	7·40
24	G vs. C	125	0·21	8·83	0·73	2·91	0·48	3·75	0·48	4·09	0·48	3·99	0·51	3·97
25	G vs. C	110	0·18	12·91	0·59	2·78	0·46	5·56	0·47	6·69	0·45	6·25	0·47	6·08
26	C vs. G	110	0·34	17·34	1·70	6·19	0·40	4·21	0·41	4·42	0·39	4·32	0·38	4·10
27	G vs. C	215	0·17	3·76	0·93	2·91	0·58	4·99	0·58	4·55	0·58	4·90	0·58	5·08
28	G vs. C	225	0·13	4·18	0·95	3·15	0·26	2·65	0·26	2·73	0·25	3·07	0·26	3·12
29	G vs. C	210	0·18	8·62	0·98	3·48	0·39	4·81	0·39	4·90	0·39	5·33	0·39	5·62
30	C vs. G	210	0·24	9·24	1·25	5·49	0·29	1·93	0·30	2·32	0·29	2·81	0·29	2·79
31	G vs. C	310	0·21	8·40	0·63	3·49	0·23	3·02	0·23	3·25	0·23	3·17	0·25	3·05
32	C vs. G	310	0·26	11·36	1·23	3·74	0·49	3·14	0·50	2·68	0·50	2·64	0·51	2·60
33	G vs. C	405	0·18	5·91	0·35	2·25	0·28	4·61	0·28	4·93	0·28	4·90	0·29	4·86
34	C vs. G	405	0·34	10·52	1·11	3·85	0·46	3·92	0·46	3·94	0·45	3·76	0·45	3·72
35	G vs. A	115	1·03	2·48	1·46	5·74	0·19	1·62	0·17	1·98	0·14	1·73	0·13	1·64
36	G vs. A	125	0·97	1·94	1·92	8·49	0·22	1·30	0·22	1·40	0·21	1·73	0·20	1·77
37	G vs. A	110	1·08	2·79	1·53	6·36	0·16	1·40	0·14	1·72	0·12	2·10	0·12	2·13
38	A vs. G	110	1·11	3·79	1·81	6·43	0·24	1·94	0·20	1·99	0·16	2·08	0·15	2·16
39	G vs. A	215	0·45	1·85	0·90	10·49	0·22	4·98	0·26	6·38	0·35	7·86	0·37	7·88
40	G vs. A	225	0·34	1·88	1·48	10·12	0·09	1·46	0·07	1·25	0·07	1·25	0·08	1·38
41	G vs. A	210	0·42	1·48	1·61	6·15	0·42	5·24	0·48	10·54	0·57	8·66	0·59	8·01
42	A vs. G	210	0·48	1·43	0·83	2·79	0·37	3·27	0·42	5·22	0·50	5·77	0·52	5·49
43	G vs. A	310	0·97	1·92	1·58	8·50	0·17	1·63	0·17	1·82	0·16	2·11	0·16	2·20
44	A vs. G	310	1·05	2·69	1·32	6·27	0·17	1·34	0·19	1·50	0·19	1·82	0·19	1·84
45	G vs. A	405	1·11	1·97	1·59	5·21	0·23	2·34	0·20	2·07	0·16	1·51	0·16	1·52
46	A vs. G	405	1·40	3·93	1·28	7·08	0·25	2·20	0·20	1·37	0·17	1·21	0·17	1·22
Nonlinear hypothesis														
47	A vs. C	110			1·29	3·40	0·85	1·61	0·91	1·76	1·02	1·88		
48	C vs. A	110			4·06	6·59	1·02	1·98	1·13	2·21	0·54	2·95		

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G. DEPENDENCE OF NONLINEAR RESULTS ON CHOICE OF PRIMARY

The dependence of the results of the nonlinear hypothesis on the choice of the green primary, specified by x_g (always taking $y_g=1-x_g$), is shown in Table 19. Data from the first observer (BURNHAM, 1957) for adaptations to illuminant A (tungsten light) and illuminant C (daylight) were used. The optimum values of A, the estimated values of their reliability w, their errors of prediction σ_s, and the ratios σ_s/σ_{vk} are listed. The values of σ_s for A vs. C indicate a minimum for $1{\cdot}4 < x_g < 1{\cdot}75$ and the values for C vs. A indicate a minimum for $1{\cdot}0 < x_g < 1{\cdot}4$. The corresponding values for the linear hypothesis are shown in the third and fourth lines of Table 10. The same trend is indicated in the third line for A vs. C. In the fourth line, for C vs. A, the minimum is at $x_g=6{\cdot}85$, but this minimum is not pronounced because the variations are so small. These results are taken to indicate that the optimum choice of primaries for the linear hypothesis is not seriously misleading for use with the nonlinear hypothesis.

The discrepancy chromaticities and the inclinations of the major axes of their covariance ellipses obtained in this study are given in the last two lines of Table 15. The half-lengths of

TABLE 17. ERRORS OF PREDICTION, MEAN DISCREPANCY CHROMATICITIES AND ADAPTATION COEFFICIENTS ON LINEAR HYPOTHESIS

Data from WASSEF (1958). Green primary is indicated by x_g as shown by column heads; except for the first column, $y_g=1-x_g$; values of σ_{vk} are to be multiplied by 10^{-4}.

	$x_g=0{\cdot}66$ ($y_g=0$)	1·00	1·40	1·75	6·85	∞
A vs. C						
σ_{vk}	528	585	564	570	576	574
$\langle x_e\rangle_{Av}$	0·25	0·32	0·26	0·27	0·27	0·27
$\langle y_e\rangle_{Av}$	0·20	0·09	0·15	0·15	0·15	0·14
θ	101°	112°	65°	71°	70°	71°
a	0·46	0·45	0·23	0·22	0·21	0·21
a/b	2·84	2·72	3·49	3·13	2·67	2·59
k_1	1·00	1·00	0·93	0·91	0·87	0·86
σ_1	0·08	0·08	0·07	0·07	0·07	0·06
σ_1/k_1	0·08	0·08	0·08	0·08	0·08	0·08
k_2	1·13	1·15	1·15	1·14	1·15	1·15
σ_2	0·10	0·09	0·09	0·09	0·09	0·09
σ_2/k_2	0·08	0·08	0·08	0·08	0·08	0·08
k_3	1·55	3·08	3·08	3·08	3·08	3·08
σ_3	0·27	0·65	0·65	0·65	0·65	0·65
σ_3/k_3	0·18	0·21	0·21	0·21	0·21	0·21
C vs. A						
σ_{vk}	410	401	363	362	364	365
$\langle x_e\rangle_{Av}$	0·39	0·54	0·45	0·45	0·45	0·45
$\langle y_e\rangle_{Av}$	0·26	0·02	0·36	0·36	0·34	0·34
θ	80°	97°	62°	67°	71°	72°
a	1·10	1·20	0·21	0·20	0·20	0·19
a/b	9·17	7·00	2·21	2·24	1·81	1·72

(The values of k for this case are the reciprocals of the corresponding values for A vs. C; the ratios of σ/k are the same.)

TABLE 18. ERRORS OF PREDICTION, MEAN DISCREPANCY CHROMATICITIES, ADAPTATION COEFFICIENTS AND OPTIMUM VALUES OF PARAMETERS FOR NONLINEAR HYPOTHESIS

WASSEF data. Green primary is $x_g = 1{\cdot}75$, $y_g = -0{\cdot}75$; adaptations are for illuminants A and C, the reversed case being treated as described for Table 2; values of σ_s are to be multiplied by 10^{-4}.

	A vs. C		Reversed	
σ_s	375		320	
σ_s/σ_{tk}	0·66		0·88	
$\langle x_e \rangle_{Av}$	0·22		0·36	
$\langle y_e \rangle_{Av}$	0·20		0·50	
θ	143°		125°	
a	0·26		0·26	
a/b	1·62		1·69	
k_1	0·98		0·95	
σ_1	0·03		0·03	
σ_1/k_1	0·04		0·04	
k_2	1·11		1·87	
σ_2	0·04		0·09	
σ_2/k_2	0·04		0·05	
k_3	1·78		1·03	
σ_3	0·09		0·05	
σ_3/k_3	0·05		0·05	
	A	w	A	w
r	0·00	7	0·95	4
r'	1·14	3	0·23	2
g	2·00	6	0·00	14
g'	0·00	4	2·00	23
b	1·93	4	2·00	9
b'	2·00	58	0·96	1

the major axes and the ratios of the major to the minor axes are given in the last two lines of Table 16.

H. SUPPLEMENTARY RESULTS

Many results not discussed or represented graphically are given in the tables for the convenience of those who may wish to test the relationships of such results with each other and with the experimental variables. Thorough study, intercomparison and plotting of various relationships of the results given in the tables convey a strong impression of the superiority of the nonlinear hypothesis.

Limitations of time and space and the small likelihood of anticipating relations in which most or even any readers will be interested, discourage the presentation here of further graphical or statistical distillations from the tables. Interested readers are urged to summarize or interpret the tabulated results in any ways that appear significant.

Many more detailed results are available than can be published. These include (1) predicted chromaticities for the corresponding colors in all cases represented in the published tables and for an average of about twenty-five preliminary sets of parameters for each of the optimized nonlinear cases; (2) errors of prediction of the tristimulus values X and Y and of the tristimulus sum S; and (3) discrepancy chromaticities, such as are plotted in Fig. 6 for only one of the over 2000 cases for which they are available. Covariance matrices are

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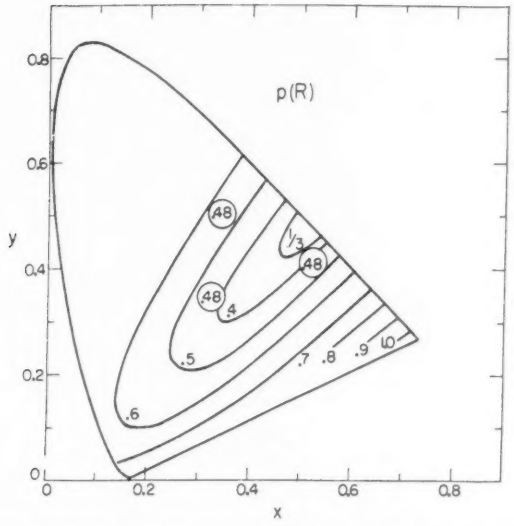

FIG. 9. Chromaticity diagram showing contours of equal p for the red response in the power form of the nonlinear hypothesis from MACADAM (1956) data. Encircled figures represent the results from BURNHAM (1952) data.

TABLE 19. DEPENDENCE ON CHOICE OF PRIMARY OF ERROR OF PREDICTION, ADAPTATION COEFFICIENTS AND OPTIMUM VALUES OF PARAMETERS FOR NONLINEAR HYPOTHESIS

Data from 10 observations of BURNHAM's (1952) observer 1. Primaries are indicated by x_g for the adaptations shown by column heads; $y_g = 1 - x_g$; σ_{vk} from Table 17. Values of σ_s are to be multiplied by 10^{-4}. Corresponding values on linear hypothesis in lines 3 and 4 of Table 10.

$x_g =$	1·00		1·40		1·75		6·85	
Adapt. =	A vs. C	Reversed	A vs. C	Reversed	A vs. C	Reversed	A vs. C	Reversed
σ_s	63	40	48	38	49	42	51	45
σ_s/σ_{vk}	0·70	0·45	0·83	0·66	0·85	0·78	0·85	0·87
k_1	1·00	1·00	0·97	0·97	0·96	0·96	0·94	0·94
σ_1	0·04	0·03	0·03	0·03	0·03	0·03	0·03	0·03
σ_1/k_1	0·04	0·03	0·03	0·03	0·03	0·03	0·03	0·03
k_2	1·05	1·06	1·04	1·04	1·02	1·03	0·99	1·09
σ_2	0·05	0·05	0·05	0·05	0·06	0·05	0·07	0·03
σ_2/k_2	0·05	0·05	0·05	0·05	0·06	0·05	0·07	0·03
k_3	1·62	1·62	1·62	1·64	1·62	1·63	1·62	1·63
σ_3	0·07	0·21	0·07	0·12	0·07	0·08	0·07	0·08
σ_3/k_3	0·04	0·13	0·04	0·07	0·04	0·05	0·04	0·06

	A	w	A	w	A	w	A	w	A	w	A	w	A	w	A	w
r	0·33	30	0·28	100	0·78	32	0·25	74	0·88	30	0·23	59	1·07	56	0·20	50
r'	0·95	40	0·57	99	0·95	36	0·57	60	0·95	25	0·38	47	0·96	32	0·15	38
g	1·24	23	1·19	37	1·25	6	0·96	10	0·99	10	0·59	2	0·00	2	0·28	0
g'	1·83	28	1·68	54	1·99	1	1·68	10	1·94	4	1·67	5	2·00	7	0·00	0
b	1·14	340	0·00	111	1·14	332	1·00	43	1·15	320	0·16	150	1·16	300	1·13	160
b'	0·78	27	0·00	70	0·78	45	0·00	59	0·85	40	0·00	6	0·83	50	0·00	45

available for all cases, but only in the form of means, standard deviations and coefficients of correlation of deviations of the discrepancy chromaticities from their means. Only the published values of axis lengths, inclinations, and ratios are available, but the simple formulas for calculating such values from the available standard deviations and correlations for all other cases can be furnished to interested workers.

Requests should be addressed to the author, who will be glad to supply any reasonable amount of specified, limited portions of the unpublished material.

Three sets of data, obtained by different experimenters using quite different arrangements and procedures and different observers, nevertheless indicate the same kinds of nonlinearity in the adaptation process, at least for adaptations to daylight and tungsten lamplight.

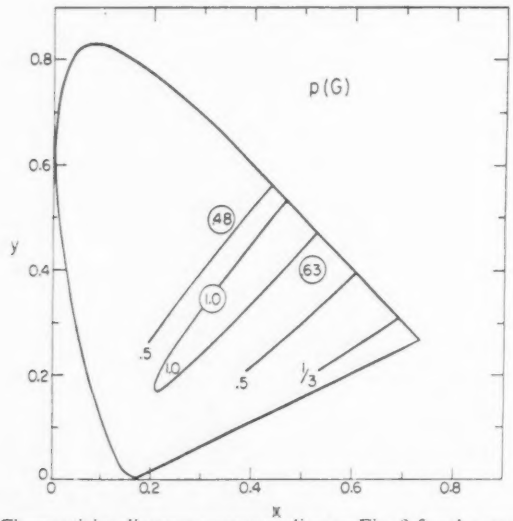

FIG. 10. Chromaticity diagram corresponding to Fig. 9 for the green response.

I. CONCLUSIONS

> Pale yellow . . . an admixture of white and auburn. White and bright meeting, and falling upon a full black, become dark blue . . . as flame color with black makes leek green.
> (Plato, *Timæus 68*, Jowett translation)

The value of p in Table 6 corresponding to each weighted mean value of A for the red response of observers DLM and EJB has been associated with the point in the chromaticity diagram representing the corresponding adaptations. The contours in Fig. 9 indicate the major trends of the dependence of these p's on chromaticity. In cases of conflicting indications, the contours have been drawn to favor the values of p corresponding to the higher precision estimates in Table 2. Since Burnham, Evans and Newhall used only three adaptations, the values of p based on their data cannot be used to construct such contours. The value based on the weighted mean value of A for all four of their observers, for each of the three adaptations, is written in Fig. 9 at the location that corresponds to the chromaticity of the adaptation. Similar contour diagrams for the values of p for green responses are shown in Fig. 10. The trends of the p's for blue responses are similarly shown in Fig. 11. General agreement among the results based on data from the six observers is indicated by these three pairs of contour diagrams and by the inscribed summary values for the observers used by Burnham, Evans and Newhall.

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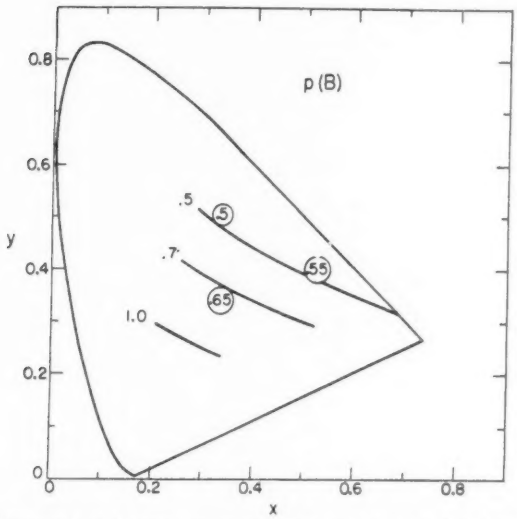

FIG. 11. Chromaticity diagram corresponding to Fig. 9 for the blue response.

Tentatively, therefore, it is suggested that colors viewed with eyes adapted to a chromaticity S corresponding to colors viewed with eyes adapted to some other chromaticity T may be calculated in terms of tristimulus values R, G and B, based on the set of primaries:

$$(x_R = 0{\cdot}747, \quad y_R = 0{\cdot}253),$$
$$(x_G = 1{\cdot}75, \quad y_G = -0{\cdot}75),$$
$$(x_B = 0{\cdot}1785, \; y_B = 0{\cdot}0)$$

by the multiplication of constant (adaptation) factors k_ρ, k_γ, k_β times

$$\rho = a_1 + b_1 R^{p(R,\,\mathrm{T})},$$
$$\gamma = a_2 + b_2 G^{p(G,\,\mathrm{T})}$$

and

$$\beta = a_3 + b_3 B^{p(B,\,\mathrm{T})},$$

and the solution of the equations

$$k_\rho \rho = a_4 + b_4 R'^{p(R,\,\mathrm{S})},$$
$$k_\gamma \gamma = a_5 + b_5 G'^{p(G,\,\mathrm{S})}$$

and

$$k_\beta \beta = a_6 + b_6 B'^{p(B,\,\mathrm{S})}$$

for R', G' and B'.

The values of $p(R, \mathrm{T})$ and $p(R, \mathrm{S})$ can be interpolated from Fig. 9 according to the chromaticities of S and T. Likewise, $p(G, \mathrm{T})$ and $p(G, \mathrm{S})$ can be interpolated from Fig. 10 and $p(B, \mathrm{T})$ and $p(B, \mathrm{S})$ from Fig. 11. The a's and b's should be assigned values such that each function intersects the Munsell Value function at about $V=1{\cdot}7$ and $V=7{\cdot}8$. The tristimulus values, R, G and B, should be normalized so that their mean values are about 20.

The factors k_ρ, k_γ, k_β should be such that S corresponds to T when $R_\mathrm{T}=20$. Values of $k_\rho\rho$, $k_\gamma\gamma$, or $k_\beta\beta$ less than a_4+b_4, a_5+b_5, or a_6+b_6, respectively, should be taken to indicate $R'=1$, $G'=1$, or $B'=1$, respectively. The method should be used only for values of k between 0·4 and 2·5.

Although no claims or suggestions of physiological significance are made, the hypothesis and method outlined are expected to reduce greatly the systematic errors of prediction that are characteristic of the linear (von Kries) hypothesis.

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PREDICTION OF RELATIVE LUMINOUS EFFICIENCY FROM FUNDAMENTAL SENSATION CURVES

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Abstract—In several recent articles (SPERLING and HSIA, 1957; SPERLING, 1958; SPERLING and LEWIS, 1959; SPERLING, 1959), I have reported data on the spectral sensitivity of the fovea obtained by different psychophysical methods, and stimulus sizes, and in various adaptive states. Those results, together with additional luminosity data obtained on dichromatic colorblind observers under some of the same conditions are summarized. The derivation of fundamental sensation curves from the color confusions of dichromatic observers (SPERLING, 1960) is presented and results of the attempted synthesis of the luminous efficiency functions from these theoretical functions are reported. These latter results are relevant to the source of the major humps and dips, the additivity law of luminances, and the general question of an additive trichromatic theory of color reception.

Résumé—Dans divers articles récents (SPERLING et HSIA, 1957; SPERLING, 1958; SPERLING et LEWIS, 1959; SPERLING, 1959), nous avons publié des données sur la sensibilité spectrale de la fovéa, obtenues par plusieurs méthodes psychophysiques pour diverses dimensions du stimulus et des états variés d'adaptation. On rappelle ces résultats, ainsi que les données recueillies sur des sujets dichromates dans certaines des mêmes conditions. On montre aussi comment on peut déterminer les courbes fondamentales à partir des confusions colorées des dichromates (SPERLING, 1960) et on expose les résultats d'un essai de synthèse des fonctions d'efficacité lumineuse à partir de ces courbes théoriques. Ces derniers résultats touchent au problème de l'origine des irrégularités principales des courbes d'efficacité, ainsi qu'à celui de la loi d'additivité des luminances et au problème général d'une théorie trichromatique additive en vision des couleurs.

Zusammenfassung—In mehreren früheren Arbeiten (SPERLING und HSIA, 1957; SPERLING, 1958; SPERLING und LEWIS, 1959; SPERLING, 1959) hat der Verfasser Daten über die spektrale Empfindlichkeit der Fovea mitgeteilt, die er durch verschiedene psychophysikalische Methoden, Reizfeldgrössen und Adaptationszustände erhielt. Mit Helligkeitsdaten, die aus Versuchen mit Dichromaten bei gleichen Bedingungen gewonnen wurden, werden diese Ergebnisse zusammengefasst. Aus den Farbverwechslungen dichromatischer Beobachter (SPERLING, 1960) werden fundamentale Empfindungskurven abgeleitet. Die Ergebnisse einer versuchten Synthese der spektralen Hellempfindlichkeitsfunktion aus diesen theoretischen Funktionen werden angegeben. Diese letzteren Ergebnisse erklären die bedeutendsten Erhebungen und Senken der Hellempfindlichkeitsfunktion, das Addivitätsgesetz der Leuchtdichten und sind bedeutsam für die allgemeine Hypothese einer additiven trichromatischen Farbempfängertheorie.

LUMINOSITY MEASUREMENT

IN 1923 a survey of the existing data by flicker photometry, the cascade method and heterochromatic brightness matching was summarized as follows by GIBSON and TYNDALL (1923): "There is no certain difference between the average values of visibility obtained by the flicker and equality-of-brightness methods, provided the former is used under the experimental conditions recommended by Ives and the latter does not depart too widely

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from these conditions." The conditions referred to as specified by the CIE in connexion with the 1924 luminous efficiency values are "a small field of fairly high-brightness". IVES (1912), in fact, settled on a 2° field of not less than 2·5 mL presented to the natural pupil. On the basis of these statements a combined set of relative luminous efficiency values from the two procedures was adopted in 1924 by the CIE. It forms a smooth, symmetrical function with a peak at 555 mμ.

In recent years doubts have arisen as to the accuracy of this CIE standard photopic function. They have involved: (a) indications that the violet region is underestimated (CIE, 1951; HSIA and GRAHAM, 1952; ISHAK, 1954), (b) the question of local irregularities in the violet, blue, and orange regions (SPERLING, 1957; HSIA and GRAHAM, 1952; WALD, 1945; SLOAN, 1928; WALTERS and WRIGHT, 1943; STILES, 1949; KINNEY, 1958) which take the form of humps and dips in the function, and (c) the question of the additivity law of luminances sometimes called Abney's law (SPERLING, 1958; DRESLER, 1953; MACADAM, 1950). This last relates the color mixture functions to the luminous efficiency function in such a way that both brightness and color matches are predicted from indirect spectrophotometric data in the CIE system. Recent work (SPERLING, 1958; SPERLING and LEWIS, 1959) with a 2° field has indicated that values obtained by brightness matching are nonlinearly related to the arithmetic sum of the color mixture functions, while those obtained by flicker photometry are estimated (within the limits of their variability) by a linear additive sum of the color mixture functions. Thus Gibson and Tyndall's conclusion that "no certain differences" exist between flicker photometry and brightness matching results for a high-brightness 2° field should be seriously re-examined. We will examine the further question of how low-brightness and absolute-threshold foveal data relate to high-brightness measurements in terms of Abney's law.

A number of interesting theoretical problems have been treated whose satisfactory solution depends upon the quantitative details of foveal spectral sensitivity. Underlying these is the general question of whether the mechanism of photopic brightness can be described as some combination of the responses to light of the individual color receptor mechanisms (additive theory) or whether a single mechanism independent of the chromatic response functions underlies photopic brightness (opponents theory). Two questions of fact, with regard to foveal spectral sensitivity, bear on this general theoretical dichotomy as well as on the practical standardization problems. First, if foveal luminosity can be predicted according to some combination of the empirically determined color mixture functions in luminosity units, support is afforded to the additive theory. This would not, however, be of general theoretical significance unless these mixture functions are generalized to a form which predicts the chromatic properties of normal and defective color vision as well.

The second related question involves the local irregularities found in various spectral sensitivity studies. It has been claimed by theorists favoring the additivity notion that these humps and dips are indications of photopic component functions and attempts have been made to derive these. This type of analysis is beset with difficulties. For one, the undoubted existence of macular pigmentation over the central retina would itself be expected to produce irregularities over the blue and violet regions (SPERLING and HSIA, 1957; HSIA and GRAHAM, 1952; WALD, 1945). Also wide variability in the number and position of humps and dips from person to person has been shown (SPERLING and HSIA, 1957). Rather than an empirical analysis of the humps and dips we offer a theoretical synthesis of rational terms based on other types of measurements such as color mixture, chromaticity discrimination, and color blindness data.

LUMINOSITY RESULTS ON NORMAL OBSERVERS

Fig. 1 presents the individual results for three observers comparing the 45′ diameter stimulus absolute threshold curves with two high-brightness curves obtained by flicker photometry and by brightness matching to a 500 troland standard. These values obtained on the same observers are more consistent in detail than was expected on the basis of

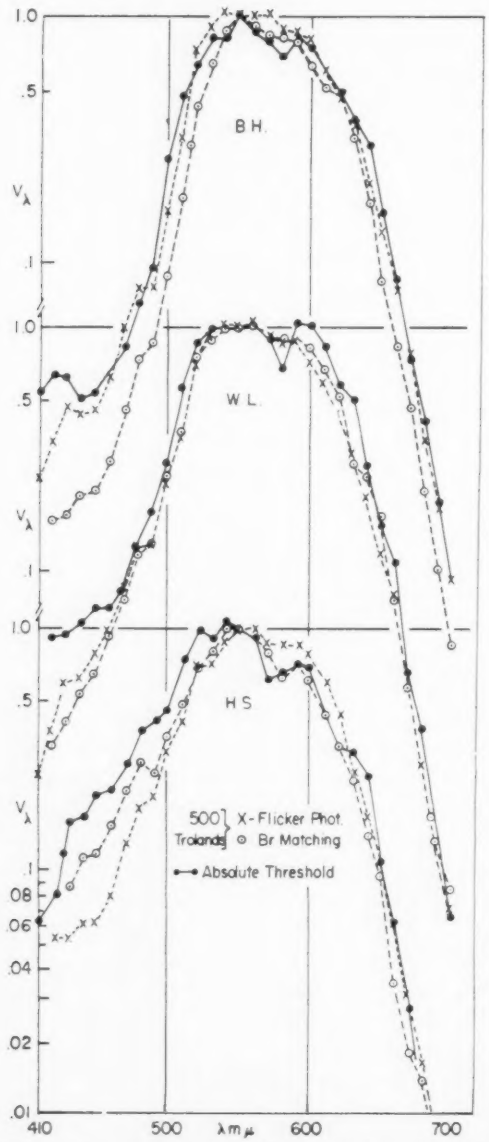

FIG. 1. Individual observers' mean spectral sensitivity functions obtained at 500 trolands by flicker photometry and brightness matching and at absolute threshold. Each observer's data has been lowered through a constant distance for ease of presentation as indicated on the ordinate (SPERLING and LEWIS, 1959).

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previous data. There are two more or less pronounced dips below 500 mμ in the three functions for all observers. There is a dip at or near 580 mμ in all curves, which produces either a peak or a shoulder at 590–600 mμ. In addition, there is some evidence of a dip at 530–540 mμ in the absolute-threshold curves which is echoed at high brightness in the flicker curve for one observer, HS. It is clear that for each observer the dip at 580 mμ is more pronounced at absolute threshold than at high brightness.

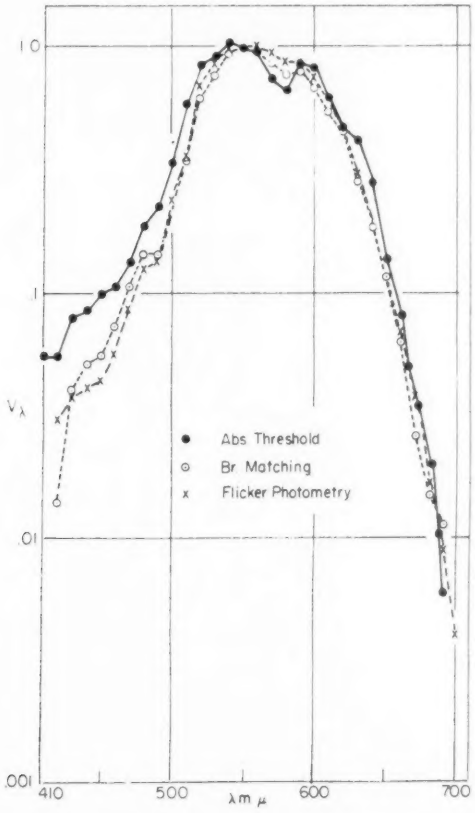

FIG. 2(a). The mean spectral sensitivity data for three observers, obtained with a 45′ diameter stimulus at absolute threshold and by two methods in a 2 500 troland field, shown on a logarithmic scale (SPERLING and LEWIS, 1959).

The average curves for the three types of measurements are shown on arithmetic and logarithmic scales in Fig. 2. In Fig. 2(b) on the arithmetic scale it is clear that brightness matching produces a more pronounced dip at 580 mμ than flicker photometry but not nearly as large as that obtained at absolute threshold. The 45′ absolute-threshold data tend on the average to be slightly higher than are the high-brightness curves in the violet-blue-green half of the curve.

The mean absolute-threshold results for the 2 diameter stimulus in the fovea are shown in Fig. 3 where the average is compared with the mean 45′ threshold curve. When the two mean curves are related in terms of energy at threshold, as was done in Fig. 3, they show

almost the same sensitivity for the longer wave part of the spectrum. The 2° function peaks at 510–520 mμ, in a way reminiscent of scotopic sensitivity curves and mixed photopic–scotopic curves which have been obtained in the periphery (KINNEY, 1958). It also shows the two irregularities below 500 mμ characteristic of other foveal data and the irregularity at 580 mμ found by high-brightness and threshold techniques. On the average, the dip at 580 mμ is much less pronounced than with the smaller foveal stimulus at threshold.

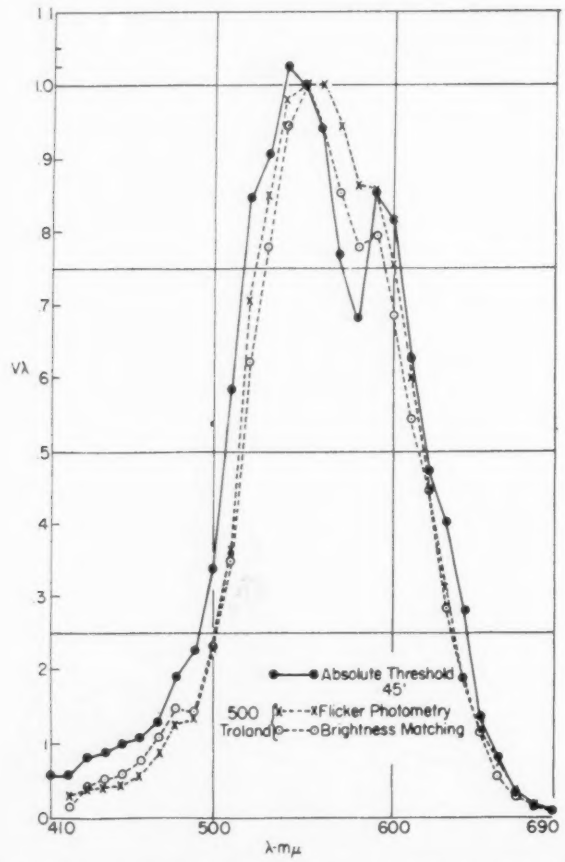

FIG. 2(b). The mean spectral sensitivity data for our three observers, obtained at absolute threshold and by two methods at 500 trolands, shown on an arithmetic scale (SPERLING and LEWIS, 1959).

The choice of 550 mμ as the wavelength at which to relate the absolute threshold and high-brightness data was a good one. When thus equated it is evident, both in the individual curves, Fig. 1, and the means, Figs. 2 and 3, that (a) they are related closely to the average peak in keeping with the conventional treatment of setting the peak to unity and (b) at the same time the entire long-wave side of the curves is brought into close agreement. This leaves the blue side of the curves showing the greatest differences between high and low brightness and 45′ and 2° stimulus sizes in keeping with the general notion of a partial Purkinjé shift (WALTERS and WRIGHT, 1943).

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Thus the Purkinjé shift within the fovea, as first reported by Walters and Wright, is found in some degree in going from high brightness to threshold even for the 45′ diameter stimulus and is found to be a considerable degree for the 2° diameter stimulus.

Let us consider the irregularities. Three major dips recur in somewhat altered form from person to person and condition to condition. They are located at 450 mμ, 490 mμ and 580 mμ. Of considerable interest is the finding that in going from high brightness to absolute threshold the 580 mμ dip becomes a deep cleft (Fig. 2(b)) which delineates twin peaks at

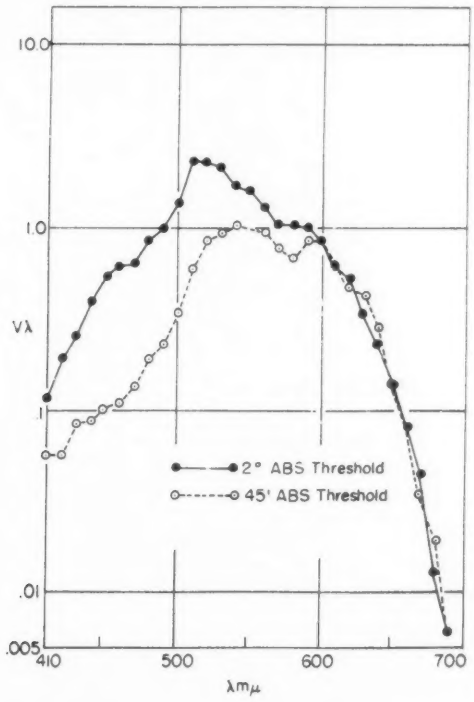

FIG. 3. Comparison of the 45′ diameter with the 2° diameter mean absolute threshold data. The curves are related by the median radiant flux density at absolute threshold (SPERLING and LEWIS, 1959).

540 mμ and 590–600 mμ. Of further interest in Fig. 3 is the fact that with the 2° diameter stimulus at absolute threshold for the same observers, this cleft does not appear but a shoulder is found similar to that found at high brightness but somewhat broader.

In a further study, now under way, we will obtain more detailed data on the behavior of the 580 mμ notch as a function of stimulus luminance. In Fig. 4, preliminary data from a single observer (BH) are shown. These were taken with a 45′ diameter stimulus in the fovea over a wide range of stimulus luminances. The lowest curve marked [A]O is the curve obtained at dark-adapted absolute threshold (seen in Fig. 1). The seven additional curves that are shown, displaced upwards by arbitrary amounts, were also computed relative to 1·00 at 550 mμ. They were obtained by flicker photometry against a dark surround to a 2900°K white-light standard having retinal illuminances: 3·0, 6·4, 22·0, 63·7, 150, 398 and 1000 trolands, for successive upwardly displaced curves. These figures, like all the others

shown, are histograms, not curves. They were obtained by connecting the mean data points with straight lines in order that absolutely no smoothing would be obtained. Thus, the curves of Fig. 4 although quite irregular in the 530–550 mμ region clearly show a gradual filling in of the 580 mμ cleft in going from absolute threshold to the higher illuminances. There is also an apparent upward shift of the peak sensitivity from 550 mμ to 560 mμ, which occurs between 64 and 150 trolands.

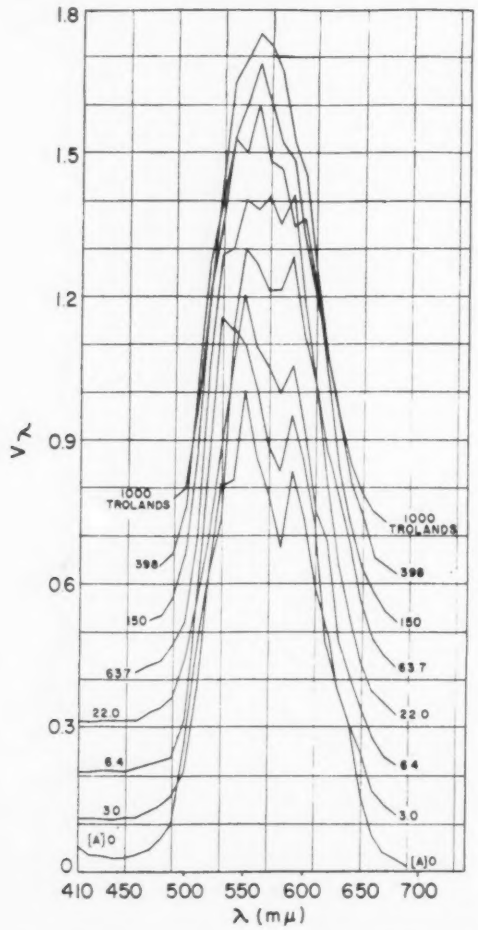

FIG. 4. V_λ curves for one observer obtained as a function of the retinal illuminance of the standard. Each curve has been set equal to 1·0 at 550 mμ and displaced from the others by an arbitrary amount.

LUMINOSITY RESULTS ON DICHROMATS

Using the technique of flicker photometry, relative luminous efficiency functions were obtained to a 500 troland standard of 2900°K color temperature on five deuteranopes and three protanopes. The relative spectral sensitivity curves are shown below in Figs. 10 and 11. The deuteranopic mean curve (10) differs from the curve for normal observers by the same

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technique at the same luminance level in that it is broader and shows lower sensitivity at the peak. Each of the five individual curves which enter this average shows some notch or irregularity in the region of 570–580 mμ. In four of the five cases this occurred at 570 mμ rather than 580 mμ (where the notch is found by these techniques with almost all normal observers, see Figs. 1 and 2).

It will be seen that the deuteranopic average curve is not equated to one at 550 mμ as was done for all curves on normal observers. Had this been done, the two tails of the curve would have fallen well above the range of normal observer data obtained by the same techniques of measurement. We are also doubtful about equating flicker photometric luminosity functions on an absolute energy basis since the luminance of the standard may vary with the loss of sensitivity. We therefore decided to equate the two on the basis of the absolute-threshold data of GRAHAM and HSIA (1958). They found that the deuteranopes and normals required the same energy to reach threshold beyond 640 mμ in the far red. So, the average of the values $V_{650-700}$ of each of our five deuteranopes was equated to the average of the values $V_{650-700}$ of the mean of six normal observers obtained under the same conditions (SPERLING, 1958). The resulting function shows a peak value of 0·659 as compared with 1·00 for the normal observer's peak value at 550 mμ. It is interesting that the results obtained by using the same apparatus and techniques on the recently studied unilateral deuteranope (GRAHAM, SPERLING, HSIA and COULSON, 1961) show an almost identical relationship of the normal eye and deuteranopic eye luminosity functions. Those data were related in terms of the radiance required for equal brightness (by flicker photometry) to the 500 troland standard.

The protanopic luminous efficiency function of Fig. 11 was obtained by flicker photometry with a 500 troland standard on three observers. The resulting mean curve is quite different from both the normal and deuteranopic functions. The peak is narrower, does not show the 580 mμ notch, but does show the slight irregularities at 460 mμ and 490 mμ.

SYNTHESIS OF LUMINOSITY FROM COLOR MIXTURE DATA

It is our purpose in this paper to test the hypothesis that photopic brightness, as measured by the luminous efficiency function, results from the combined response of the chromatic receptors. In a recent article (SPERLING, 1960), the author derived a set of fundamental response curves by assuming, as Helmholtz had (SOUTHALL, 1924), that the convergence points of the confusion lines[1] of protanopes and tritanopes is a representation of the chromaticity of the missing receptors associated with the "blue" and "red" receptor processes of trichromatic theory. A third point to represent the "green" process was determined in accordance with the Fick–Leber hypothesis by assuming the fundamental sensation triangle to be the smallest triangle which would bound the locus of all spectral colors and have the tritanopic and protanopic points as two of its corners. According to the Fick–Leber hypothesis, deuteranopes are not missing a receptor mechanism but the mechanisms for red and green are somehow fused so that they cannot act independently.

Helmholtz showed that in the latter case the confusion lines would converge at infinity. PITT (1935) and MacAdam (*ibid.*) have pointed out that parallel lines would be predicted by the Fick–Leber hypothesis only in the special case of equal response "red" and "green" systems. In all other cases a finite locus of origin for the confusion lines should be found

[1] Lines in a chromaticity plane connecting the coordinates of two colors which are confused by a dichromat.

which would lie further from the spectrum locus than the point which would represent a missing receptor.

The plane shown in Fig. 5 is a transformation of the 1931 CIE tristimulus values to the primaries determined by the loci of origin, B' and R', of the confusion lines of tritanopes and protanopes. G' was arrived at as the point which would complete the smallest triangle which bounds all spectral colors. In the triangle of Fig. 5, one additional assumption was made in order to have a completely determined plane. The point for equal energy was transformed so as to equate the number of just noticeable differences from it to blue with

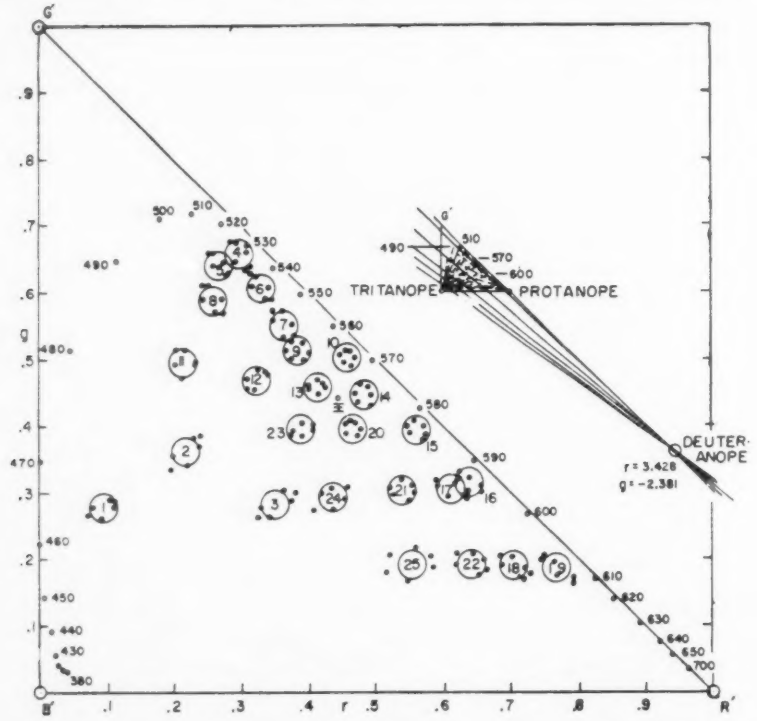

FIG. 5. The *RG* chromaticity plane derived from the 1931 CIE tristimulus values by linear homogeneous transformation according to equations (1)–(3). Shown as dots are six points on each of MacAdam's J.N.D. ellipses. The color confusion lines of the three classes of dichromats in this plane are shown in the insert.

those to yellow. The result was a plane which closely approximated several equal chromaticity difference planes, at the same time that it incorporated data on protanopia, tritanopia, and the Fick–Leber version of deuteranopia. In addition, the plane predicts that spectral stimuli, in the region of 460 mμ and in the region of wavelengths longer than 575 mμ, are at, or very close to, their theoretically maximum saturations. WRIGHT's studies (1947) on chromatic adaptation support this view.

In the present work, where we are interested in predicting luminous efficiency as some combination of the transformed tristimulus values, it seemed more sensible to base the synthesis on our own tristimulus measurements which provide exact experimentally determined luminosity coefficients. Our luminosity coefficients could be transformed by

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exact techniques to refer to new primaries. Also those data were made under comparable conditions to those for most of the luminosity curves presented above (SPERLING, 1958). A chromaticity diagram was constructed by transforming coordinate points arrived at by the intersection of the color confusions and by the minimum triangle concept to the orthogonal coordinates 0,0; 0,1; 1,0. The resulting fundamental sensation curves differ only slightly from those on which Fig. 5 is based. They are shown in Fig. 6.

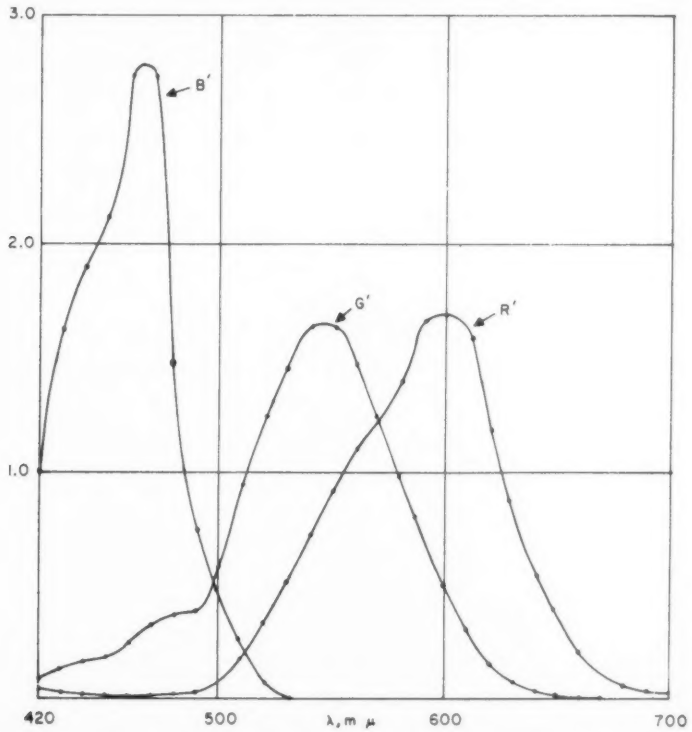

FIG. 6. The tristimulus functions R', G' and B' obtained by transforming the color matching data (SPERLING, 1958) to theoretical primaries as determined by the confusions of dichromats.

The luminous efficiency weightings of the working primaries were transformed by exact equations, as described by JUDD (1931). That operation resulted in the same relationships between SV_λ, the sum of the weighted, transformed tristimulus values and V_λ, as had obtained between the working primaries and V_λ. These transformations may be summarized after Judd as:

$$R' = a_1R + a_2G + a_3B \tag{1}$$

$$G' = a_4R + a_5G + a_6B \tag{2}$$

$$B' = a_7R + a_8G + a_9B \tag{3}$$

where R, G and B are the tristimulus functions (primaries: 460, 520 and 650 mμ). R', G' and B' are the new rational primaries arrived at via the theoretical considerations described above.

a_1–a_9 were derived such that $\begin{vmatrix} a_1 & a_2 & a_3 \\ a_4 & a_5 & a_6 \\ a_7 & a_8 & a_9 \end{vmatrix} \neq 0$ (4)

In the usual statement of the relationship between luminosity V_λ and the tristimulus values an additive relationship is presumed where

$$V_\lambda = V_R R + V_G G + V_B B \tag{5}$$

This is sometimes called Abney's law (see JUDD (1955) for the history of this relationship). In the new rational primaries:

$$V_\lambda = V'_R R' + V'_G G' + V'_B B' \tag{6}$$

where V'_R, V'_G, V'_B are determined from the experimental V_R, V_G and V_B as follows:

$$V'_R = 1/\Delta \left[V_R \begin{vmatrix} a_5 & a_8 \\ a_6 & a_9 \end{vmatrix} + V_G \begin{vmatrix} a_7 & a_4 \\ a_9 & a_6 \end{vmatrix} + V_B \begin{vmatrix} a_4 & a_7 \\ a_5 & a_8 \end{vmatrix} \right] \tag{7}$$

$$V'_G = 1/\Delta \left[V_R \begin{vmatrix} a_8 & a_2 \\ a_9 & a_3 \end{vmatrix} + V_G \begin{vmatrix} a_1 & a_7 \\ a_3 & a_9 \end{vmatrix} + V_B \begin{vmatrix} a_7 & a_1 \\ a_8 & a_2 \end{vmatrix} \right] \tag{8}$$

$$V'_B = 1/\Delta \left[V_R \begin{vmatrix} a_2 & a_5 \\ a_3 & a_6 \end{vmatrix} + V_G \begin{vmatrix} a_4 & a_1 \\ a_6 & a_3 \end{vmatrix} + V_B \begin{vmatrix} a_1 & a_4 \\ a_2 & a_5 \end{vmatrix} \right] \tag{9}$$

where

$$\Delta = \begin{vmatrix} a_1 & a_2 & a_3 \\ a_4 & a_5 & a_6 \\ a_7 & a_8 & a_9 \end{vmatrix} \tag{10}$$

If we now substitute the term SV_λ for the left hand side of equation 6 and compare SV_λ with the V_λ function by flicker photometry (at 500 trolands) (Fig. 7) we find very close agreement, indicating that Abney's law is closely upheld for that condition of measurement. One serious difficulty arises, however. The value for V'_B comes out negative. If our assumptions are correct in arriving at this transformation, this could be interpreted as saying that while the blue mechanism plays a positive role in determining the degree chromaticity, it plays a negative or inhibitory role in determining brightness. There is some general supporting evidence for such a conclusion, but before considering this more drastic interpretation of the negative V'_B let us look at another possibility. The color mixtures on which the tristimulus values are based were obtained with a 2° centrally fixated match field. The flicker photometric V_λ's were obtained with half this field blocked off and the eye fixating the center of the resulting semicircle. The macular pigmentation of the eye acts as a filter which reduces the amount of blue light reaching the foveal receptors. The density distribution as a function of wavelength also closely coincides with the B' function. So that if it could be said that the centrally fixated semicircle encountered a higher average density of pigment over its area than the full 2° match field, there would be a basis for saying that the blue (V'_B) luminosity weighting should be smaller, perhaps zero or slightly positive, and that the discrepancy with the flicker photometric V_λ function results from a difference in the percentage pigment filtering the differently sized fields. We will attempt this approach in the following treatment.

Before examining the degree of success in predicting V_λ from the transformed tristimulus values, let us state a more general equation which will be used throughout for the synthesis of luminosity. It is a generalized form of Abney's law.

$$SV_\lambda = \{t_\lambda{}^x[(V'_R R'_\lambda)^n + (V'_G G'_\lambda)^n + (V'_B B'_\lambda)^n]^{m/n} + [t_\lambda{}^x CS'_\lambda]^m\}^{1/m} \tag{11}$$

where t_λ is the transmittance of unit concentration of the macular pigment, x the actual concentration of t, S'_λ the CIE *scotopic* luminosity function-representative of a "rod vision" term and R'_λ, and G'_λ and B'_λ the tristimulus values referred to our theoretical primaries. SV_λ is predicted or synthetic luminosity, in terms of the three or four component functions.

The exponents m and n are a means of representing different degrees of summation between the photopic and scotopic components (m) and within the photopic (n). C is related to the rod–cone population ratio and should vary with stimulus area and position as well as state of adaptation. V'_R, V'_G, V'_B are the luminous efficiencies of unit energy amount of the primaries R', G', and B'.

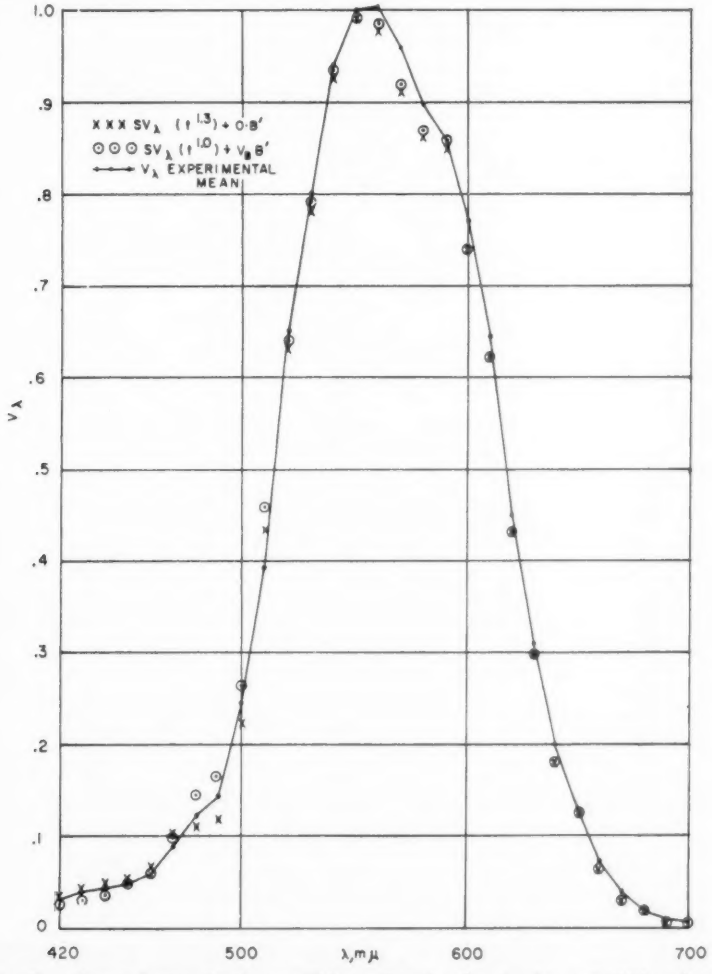

FIG. 7. Experimental mean luminous efficiency function for six observers (V_λ) and attempted synthesis (SV_λ) from fundamental sensation curves according to equation 11. Two SV_λ's are shown. The open circles represent the exactly transformed experimental luminous efficiencies of the primaries while the crosses represent the assumption of "zero" spectral luminous sensitivity of the "blue" mechanism.

Obviously, many will say that with all these variables, coefficients and exponents, it should be possible to fit closely any luminosity curve. Our answer is that the inclusion of each of these terms follows the dictates of additive trichromatic theory and of the known anatomy and physiology of color and brightness vision. In the case of each term (save the exponents m and n) the possibility of determining the value of the coefficients by separate

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measurements exists. The V'_R, V'_G, V'_B values should vary with the dark-adaptation of the hypothesized R', G', B' receptors and might be estimated from data on monochromats or from extreme chromatic adaptation studies. C should vary with data on the density and size of the rods and cones stimulated. The function t has been measured by WALD (1945)

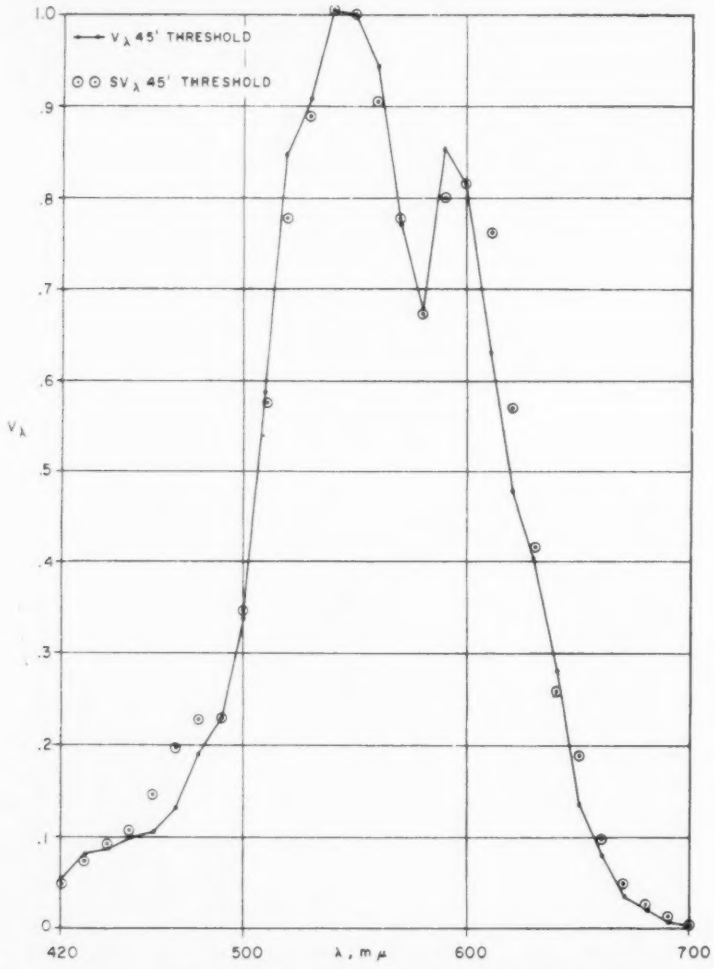

FIG. 8. A comparison of the mean V_λ data for the centrally fixated 45′ diameter stimuli at absolute threshold in the fovea with SV_λ of equation 11 using $n=50$.

and its distribution plotted by MILES (1954). We have plans to evaluate x by determining the threshold of the Maxwell spot. In any case, it will be instructive to see if even this number of seemingly rationally based terms will adequately predict the variety of luminosity functions reported above.

Fig. 7 compares the V_λ obtained by high brightness flicker photometry using the 2° diameter semicircular stimulus in the fovea with SV_λ of equation 11 obtained by taking V'_R, V'_G and V'_B exactly as transformed from experimental values according to equations 7, 8, 9 and 10. The value of C was taken as zero (no rods present). In the best-fitting

curve it was found that $n=1$, indicating complete arithmetic summation. A second set of SV_λ values is shown (in Fig. 7) with V'_B taken as zero rather than negative and x taken as 1·3. The function x was taken as unity in the negative set. The assumption of no contribution of the "blue" mechanism to luminosity is, of course, a simpler one since it does not require an inhibitory mechanism. On the other hand, considering the extreme variability of

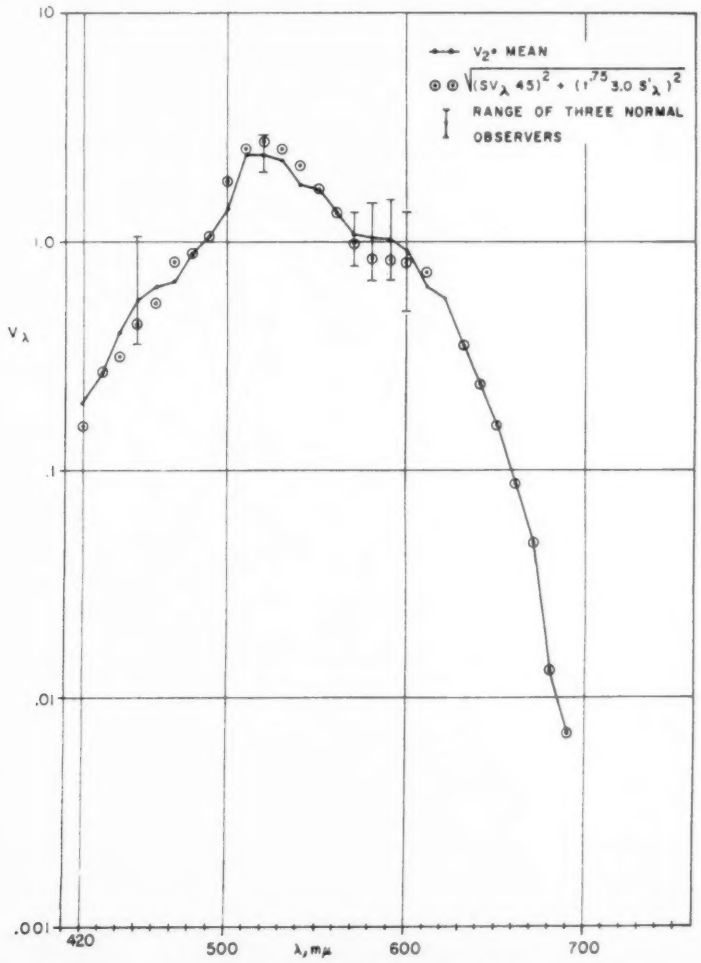

FIG. 9. A comparison of the mean V_λ data for the centrally fixated 2° diameter stimulus at absolute threshold with SV_λ from equation 11, using a positive value of C, $n=50$, $m=2$.

both the pattern and the density of the macula lutea (MILES, 1954) and of V_λ measurements in the 400–500 mμ region, little basis for a choice between the two assumptions is available. It appears that a nearly equal fit to the data is obtained by either assumption.

Fig. 8 shows the average data obtained with the 45′ diameter stimulus, at absolute threshold compared with SV_λ taking $n=50$. V'_B is again assumed equal to zero on the assumption of no "blue" contribution to luminosity. It is clear that the deep cleft at 580 mμ could not be fit by any variation of coefficients applied to the R' and G' variables, but

requires the very large value of n, which implies little or no summation between the R' and G' mechanisms at absolute threshold. In fact, under this condition V_λ may be fitted by the peaks of the individual R', G' functions adjusted to cross at 580 mμ, indicating no summation whatever. Going back to the series of V_λ functions shown in Fig. 4, for one observer it is

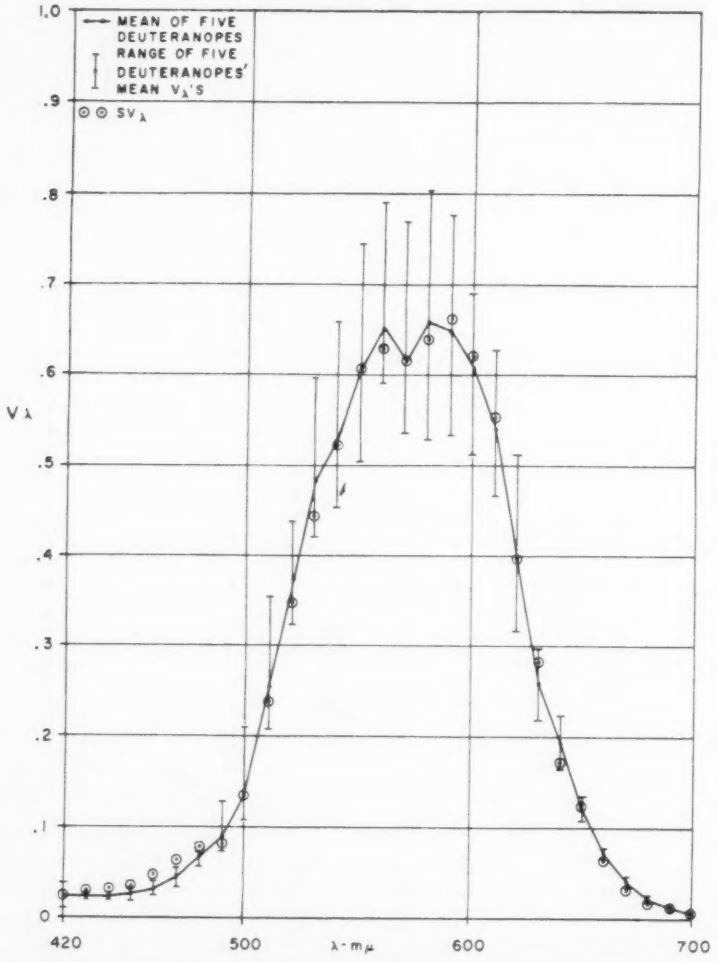

FIG. 10. A comparison of the mean and range of V_λ for five deuteranopes with SV_λ of equation 11, taking $V'_B=0$, V'_G equal to 0·45 of its value for normal observers and V'_R equal to its value for normal observers; $n=1$.

evident that there is a gradual increase in summation, going from absolute threshold to high brightness. Work is now under way to develop analytical procedures to find the best values of n, V'_R and V'_G to fit the (average) data from several observers now being gathered in this experiment.

In Fig. 9, the V_λ curve obtained by stimulating the 2° central area at absolute threshold is compared with SV_λ from equation 11. It will be recalled from Fig. 3 that the cleft found with the smaller stimulus at absolute threshold became a flattened shoulder with the 2° stimulus

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at the same time that the peak shifted to 510 mμ. Now, by using a value greater than zero for C (equation 11) we are able to add in the S' "rod" curve. We find it possible to shift the peak to a close fit at the same time that a quite similar shoulder instead of a cleft is obtained. In predicting rod–cone summation for the fovea it is necessary to weight S' (which was measured at 10° in the periphery) with t^x, the transmittance of the macula lutea. A value of $x=0{\cdot}75$ was found to give the best fit. A value of $m=2$ was used here, as had been found by Stiles to describe the degree of rod–cone summation. No attempt to find optimum value of V'_R, V'_G and V'_B was made here. The values from the 45′ data at threshold (Fig. 8) were

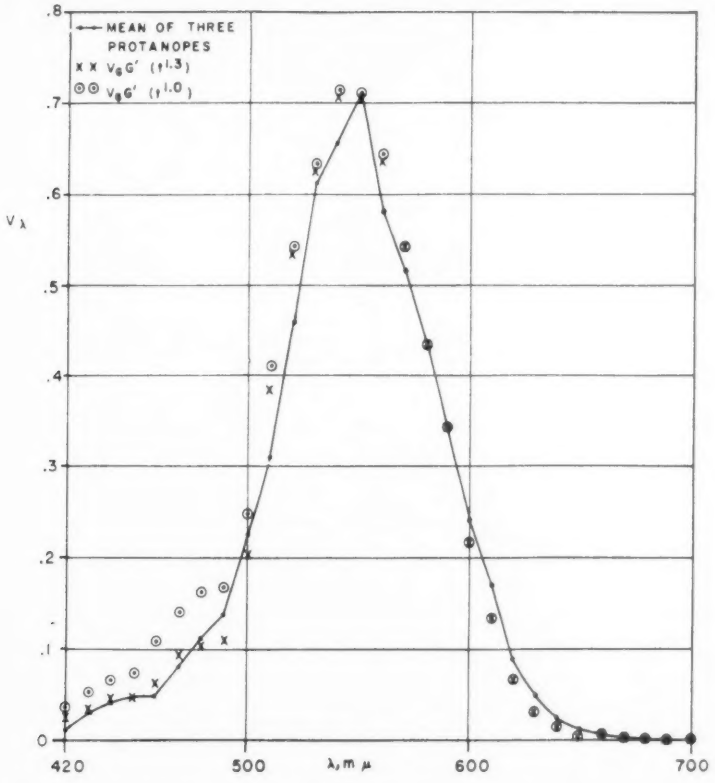

FIG. 11. A comparison of the mean V_λ for three protanopes with SV_λ of equation 11, taking $V'_B=0$, $V'_R=0$ and V'_G equal to the value for normals. Data for two different values of x, the concentration of the macula lutea are shown.

used. If a somewhat larger value of V'_R had been used (in keeping with the notion of a changing population density of chromatic receptors across the retina) a somewhat better fit in the region of the 580–610 shoulder might have been accomplished. We feel, despite this discrepancy, that one of the most promising of our results is the ability to duplicate the change in shape of the 580 mμ cleft by this partial summation with the scotopic S' function.

Fig. 10 presents the mean high-brightness flicker photometric data obtained on deuteranopes compared with SV_λ (from equation 11) with $C=0$, $n=1$, V'_B, V'_R the same as used for normals and V'_G taken as 0·45 times the value found for the normal observers. It will be noticed that we are able to predict the shift from 580 mμ to 570 mμ that was found in the

average V_λ data by assuming that R' and G' summate completely, as in normal observers at this stimulus illuminance and that the G' receptors are about half as numerous (or sensitive). Thus, deuteranopic luminous efficiency may be described by assuming a 55 per cent loss of sensitivity of the G' function and that all other terms are identical with normals. This result

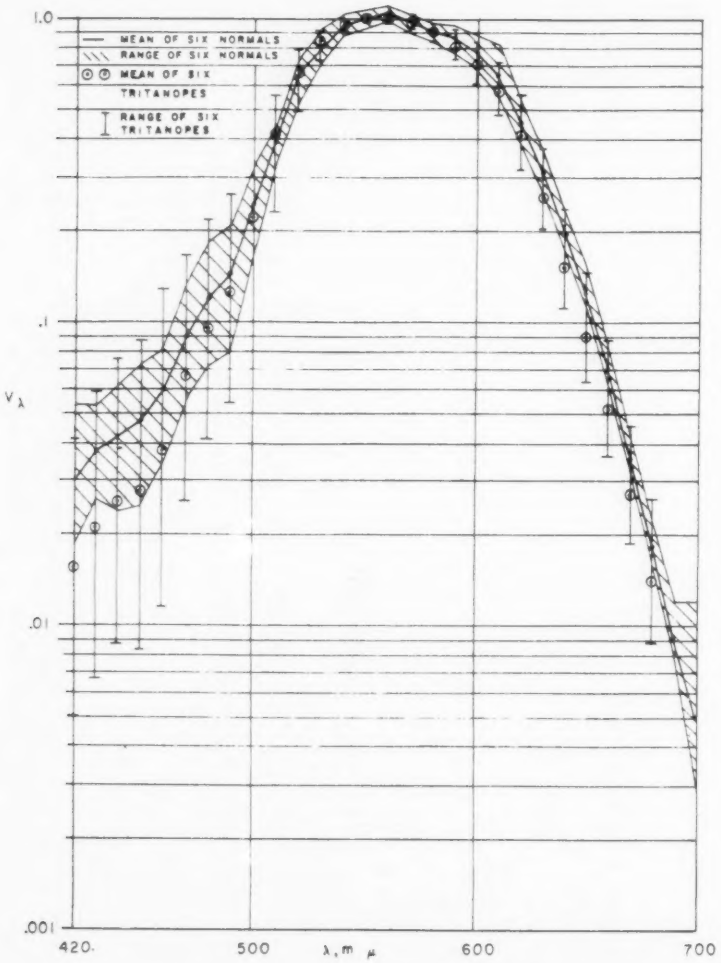

FIG. 12. A comparison of the mean and range of V_λ for six normal observers (of Fig. 7) with the mean and range of V_λ for six tritanopes (WRIGHT, 1952).

and the inability of deuteranopes to discriminate red from green lead us to propose that deuteranopia involves either an abnormal and less efficient neural linking of the "red" and "green" pathways or the location of the photochemical substances in the same receptors, not the existence of an intermediate photochemical substance as has been suggested by GRAHAM and HSIA (1958).

Fig. 11 compares the mean high-brightness data for our protanopes with SV_λ. Here, the two curves are arbitrarily tied together at 550 mμ. This SV_λ resulted from taking V'_G equal

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to the value for normal observers and $V'_B=0$; $V'_R=0$. The coefficient C was taken as zero since these were high-brightness data. The concentration of macular pigment was varied to obtain the optimum fit. A concentration of 1·3 was found to give the best fit of those tried. It is clear here, and in good agreement with previous findings, that protanopia involves a complete absence of red receptor function. R' appears to be a good estimate of that function as does G' of the remaining green sensitivity, provided of course that our assumption of no luminous contribution from the blue receptors is valid.

In the last figure (Fig. 12) some evidence is given which supports the assumption that blue should have zero luminous efficiency. There WRIGHT's (1952) average data and the ranges for six tritanopes are shown and compared with the data on the six normals on which Fig. 2 is based. It is clear that tritanopia, which meets the criteria discussed above for a missing blue receptor since the confusion lines converge on a well-defined point very close to the spectrum locus, displays no significant loss of sensitivity over the blue end of the spectrum.

DISCUSSION

In the work presented here and by SPERLING (1960), we have attempted to carry through a self-consistent, quantitative statement of the color mixture, luminosity and chromaticity discrimination functions of normal observers and the color mixtures and luminosity functions of dichromatic observers. The unifying themes have been the additive trichromatic theory of Helmholtz and the Fick–Leber hypothesis. Quite similar attempts have been made by THOMSON and WRIGHT (1953) and PITT (1944) on the basis of the confusion loci of dichromats, but were not carried out with knowledge of recent advances in one or more of the following: data on the humps and dips in the luminosity curve, confusion data on congenital tritanopes and findings on the loss of luminosity in deuteranopes. It is felt that additive trichromatic theory does a good, but not perfect, job of predicting the data shown here on the spectral sensitivity of the foveae of normal and dichromatic observers. It does so in a way, however, which is consistent and which permits verification by experimentation. The seemingly *ad hoc* manipulation of the macular pigment concentration, in order to avoid negative blue coefficients, appears to be the weakest spot in the treatment. The failure to make better than "trial-and-error" predictions of chromaticity discrimination as shown in Fig. 5 is another weakness. It should be remembered, however, that, except for the pigment manipulation, the simplest assumptions have been made consistent with the basic theoretical concepts. It would have been possible to provide a better fit to discrimination data with a three-dimensional color-brightness space and the concept of inhibition of luminance could have been introduced to account for the discrepancy in the blue. The idea throughout, however, was to make a very simple application of the theory and to see how well it predicts not only the data of color mixture, color discrimination and the general aspects of luminosity, but also the additional information on the luminosity loss of deuteranopes and the dip in the luminosity curve near 580 mμ. This notch appears to be of definite analytical significance. The way in which equation 11 is able to predict changes in the notch shape with changing size of the stimulus and different states of adaptation of the eye is the strongest result of the foregoing analysis. The way in which the 460 mμ and 490 mμ notches reappear practically unaltered, throughout the various conditions and defects, leads us to agree with Wald "that they result from absorption peaks in the macular pigment".

The possibility exists that the discrepancies with the discriminations shown in Fig. 5 would decrease if more than one observer's discriminations were available, especially if the

color mixture data were obtained on the same observers. It should be noted that both the color mixture and luminosity data were gathered on quite small samples. Our future plans include experiments on color mixture and relative spectral sensitivity as a function of stimulus luminance, and chromaticity discrimination on the same observers.

On the specific question of the additivity of heterochromatic luminances it was noted previously (SPERLING, 1958; SPERLING and LEWIS, 1959) that the failure of the sum of the weighted tristimulus values (SV_λ, equation 5) to predict measured V_λ was coincident with the region of the 580 mμ dip. The sum SV_λ overestimated V_λ in that region. By introducing the exponent n in equation 11 we have provided for variable summation of the R' and G' terms which quite successfully predicts this region in the two extremes of high brightness, where Abney's law ($n=1$) appears to hold and absolute threshold where a very large n provides a good fit indicating little or no summation. The data of Fig. 4 for intermediate stimulus levels indicate that there is a continuous variation of the depth of the notch from threshold through intermediate to high luminances. We conclude from this that not until we reach very high troland values can we expect Abney's law to hold. The statement of equation 11 is proposed as a more general expression with which we expect to be able to predict intermediate luminances from tristimulus values.

Acknowledgement—The experimental work reported here was conducted when the author was employed in the U.S. Naval Medical Research Laboratory, Submarine Base, New London. The program was conceived with the advice and encouragement of the late COMMANDER DEAN FARNSWORTH. I recall with fond memories and a real sense of loss the sharp and probing criticisms which Dean produced in our many conversations on these and related topics. I am sure this would have been a better paper had it the benefit of his detailed and understanding comments. It was this type of basic psychophysical research on normal and deficient color vision which Dean envisioned and planned for when he set up a basic research section and arranged to acquire the Fry colorimeter. For years he fought off "applications-minded" criticism of this and related basic studies while I, and others in my section, fumbled through learning the intricacies of radiometry, spectral calibration and the many other time-consuming and expensive physical preparations which were necessary. I wish that we had more to show for the good battles which he fought.

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ROD AND CONE RECEPTOR MECHANISMS IN TYPICAL AND ATYPICAL CONGENITAL ACHROMATOPSIA[1]

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Abstract—Spectral sensitivities and interactions of the receptor systems of thirteen congenital achromats with reduced acuity were determined by psychophysical measurements with white and blue light. Patients were of three categories: (1) rod monochromats: functioning rods only; (2) blue monocone monochromats: blue-sensitive cones (maximum at 440 mμ) and foveal rods with normal scotopic curve modified by the absorption of macular xanthophyll; these patients function as blue cone monochromats at high luminances, as rod monochromats at low luminances, and as blue cone–rod dichromats at intermediate luminances; and (3) intermediates, with rods and blue cones of insufficient number for color discrimination. All patients are believed to have the same receptor systems. Differences in fixation seem to explain the functional differences.

Résumé—Les sensibilités spectrales et les interactions des systèmes de réception de treize achromatopes congénitaux avec une acuité réduite ont été déterminées par des mesures psychophysiques en lumières blanche et bleue. Les malades se partagent en trois classes: (1) les monochromates de bâtonnets: les bâtonnets fonctionnent seuls; (2) les monochromates de monocônes bleus: les cônes sensibles au bleu (maximum à 440 mμ) et les bâtonnets fovéaux avec la courbe scotopique normale modifiée par l'absorption de la xanthophylle maculaire; ces derniers fonctionnent comme monochromates de cônes bleus aux luminances élevées, comme monochromates de bâtonnets aux luminances faibles, et comme dichromates de cônes bleus et bâtonnets aux luminances intermédiaires; et (3) les malades intermédiaires, avec des bâtonnets et des cônes bleus insuffisants pour distinguer les couleurs. On pense que tous les malades ont les même systèmes de réception. Les différences dans la fixation semblent expliquer les différences fonctionnelles.

Zusammenfassung—Der Zusammenhang zwischen Receptorensystem und spektraler Empfindlichkeit wurde bei dreizehn Patienten mit congenitaler Achromasie und herabgesetzter Sehschärfe durch psychophysikalische Messungen mit weissem und blauem Licht untersucht. Drei Gruppen von Patienten wurden unterschieden: (1) Stäbchen-Monochromaten: lediglich Stäbchenfunktion; (2) Blauzapfen-Monochromaten: blauempfindliche Zapfen (maximale Empfindlichkeit bei 440 mμ) und foveale Stäbchen mit normaler scotopischer Empfindlichkeitskurve, modifiziert durch die Absorption von Macula-Xantophyll. Diese Patienten verhalten sich bei hohen Leuchtdichten wie Blauzapfen-Monochromaten, bei geringen Leuchtdichten wie Stäbchen-Monochromaten und bei mittleren Leuchtdichten wie Blauzapfen-Stäbchen-Dichromaten; (3) Zwischenformen, die eine ungenügende Anzahl von Stäbchen und Blauzapfen besitzen um Farben unterschieden zu können. Es wird angenommen, dass alle Patienten dasselbe Receptorensystem haben. Das unterschiedliche Verhalten scheint auf Differenzen beim fixieren zu beruhen.

[1] The studies upon which this paper is based were made while the authors were associated with the Vision Research Laboratories at The University of Michigan, and were supported by the Knights Templar Fund. The data analysis was carried out at The Ohio State University as a cooperative project with the Department of Ophthalmology, and was supported by the Ohio Lions Eye Research Foundation and by Public Health Service Grant B2201.

INTRODUCTION

IN RECENT years, there has been a renewed interest in congenital achromatopsia, due to the discovery of what have been designated atypical cases. Typical congenital achromatopsia is usually assumed to result from the complete absence of functioning cone photoreceptors, all functional characteristics of this abnormality being produced by rod photoreceptors alone. The visual acuity of patients with this abnormality is usually less than twenty in a hundred, there is a complete absence of hue-discrimination, and spectral sensitivity peaks at about 510 mμ. There may or may not be photophobia and/or nystagmus.

One type of atypical congenital achromatopsia reported by PITT (1944) exhibited normal or supranormal visual acuity, with spectral sensitivity peaking at about 540 mμ, but with a complete absence of hue-discrimination. This patient is believed to have at least one type of cone and is clearly very different from the typical achromat.

A second type of atypical congenital achromatopsia has been reported (JAEGER, 1953; SLOAN, 1954; FRANCOIS and VERRIEST, 1959) with visual acuity of about twenty in sixty, which seems too high for a purely rod system. Some patients in this category give evidence of at least rudimentary hue-discrimination. Detailed study of these cases led JAEGER (1953) to conclude that cone and rod photoreceptors were present in at least some cases.

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The confusion arising from designation of these two classes of patients by the term atypical congenital achromatopsia led the present authors (BLACKWELL, H. R. and BLACKWELL, O. M., 1957 and 1959) to describe cases of achromatopsia with compound terms, the first describing the number and type of receptor systems found to be operative. Thus, there may be rod monochromacy. At the other extreme, there may be tricone monochromacy in which red, green, and blue cones are present, the patient nonetheless having a monochromatic functional system. Or, there may be dicone monochromacy in which two cone systems are present, or monocone monochromacy in which only one cone system is in operation. The use of this compound nomenclature implies, of course, that sources of evidence other than chromatic discriminations can be found which will identify the number and spectral characteristics of the receptor systems present. The literature suggests that luminosity (HSIA and GRAHAM, 1957), the acuity function of luminance (HSIA, HECHT and SHLAER, 1950), and the effect of chromatic adaptation on acuity (BRINDLEY, 1953) provide useful indices of the cone mechanisms in operation, independent of the patient's ability to make chromatic discriminations. Luminosity will of course identify the presence of a purely rod system.

The present series of studies was initiated when three brothers were encountered in the clinic who appeared to have congenital achromatopsia but whose visual acuity was about twenty in sixty. This acuity level was considered too high for typical achromatopsia and efforts were made to study the functional characteristics of these "atypical" patients. Measurements were made over a period of nearly three years (BLACKWELL, H. R. and BLACKWELL, O. M., 1959), during which time suitable equipment and procedures were developed and refined. When these measurements were well along, patients with the symptoms of typical congenital achromatopsia were sought for purposes of comparison. Extensive psychophysical data have been obtained on nine male cases representing either typical or atypical congenital achromatopsia of the reduced acuity type. Summary data for eight cases will be presented in terms of three functional categories derived from the psychophysical data obtained. The data for the remaining patient and for four male siblings of the affected patients will be related to the three functional categories used to describe the first eight cases.

APPARATUS AND PROCEDURES

All patients were given a detailed ocular examination by Dr. Harold F. Falls of the Department of Ophthalmology at The University of Michigan. This included external, refraction, field, and fundus examinations. In addition, family histories were obtained on most patients by The University of Michigan Heredity Clinic.

The present authors were responsible for the psychophysical examinations made on the patients. Special equipment was developed for measuring spectral sensitivity, dark-adaptation, and the acuity function of luminance. In addition, the color vision of each patient was examined utilizing standard equipment including pseudo-isochromatic plates, the Farnsworth–Munsell 100-Hue Test, and a Nagel-type Anomaloscope. Since the color vision tests provide less information than our other measurements, the results of these will be omitted.

Spectral sensitivity was defined by the determination of luminosity coefficients for various wavelengths. These coefficients were determined with a special spectral comparator, based upon a Hilger-prism monochromator, which has been described elsewhere by our late colleague PRITCHARD (1958). Radiometric measurements were made of the output of the device at various wavelengths, and cut-off filters were used to eliminate the spectral stray light which would otherwise have invalidated our measurements. Spectral transmittance measurements were made on various so-called neutral filters and wedges used to modify the radiant energy. The spectral comparator was used first by the present authors (BLACKWELL, H. R. and BLACKWELL, O. M., 1959) to measure luminosity functions on normal observers, and an optimal luminosity technique was developed. A standard source of 402 mμ was usually used and each patient was required to match other wavelengths of the spectrum to this standard. Matches were always verified after adaptation to a white light of matched luminance, so as to minimize the possibility of chromatic adaptation. For normal subjects, it was found desirable to reduce color differences between the standard and comparison fields by a modified "cascade method", involving use of a series of standards spaced across the spectrum. For the present patients, initial use of this procedure demonstrated that the patients had little difficulty matching the luminances of all wavelengths against a single standard, so that the patients were usually required to match the luminances of all wavelengths against the 402 mμ standard. Measurements obtained with the two methods were found to be equivalent and the two types of data have been used interchangeably throughout the present report.

In our spectral comparator, the photometric cube is of the concentric ring variety. The piameter of the inner field, containing the spectral comparison, subtended 30′, and the piameter of the outer field, which comprised the standard, subtended 1 . The device incorporates an artificial pupil smaller than the minimum natural pupil of any patient, so that it is possible to compute the retinal illuminance produced by the standard when set at various radiance levels. A special lens is used (VAN HEEL, 1946) to reduce difficulties due to ocular chromatic aberration. During the luminosity measurements, the patients were asked if they could obtain perfect matches between various spectral stimuli and the 402 mμ standard. Insofar as they were able to obtain perfect matches, it can be concluded that the patients were without chromatic discrimination.

The illuminance level at which the luminosity determinations were made could be varied by altering the radiance of the initial standard used, by means of filters and wedges. In each case, the retinal illuminance (E_r) was computed from the radiance of the initial standard by the equation:

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$$E_r = 2{\cdot}58 \times 10^4 \; V_s \; N_s \tag{1}$$

where E_r is expressed in trolands;

N_s is the radiance of the initial standard in watts per square foot per steradian per millimicron;

V_s represents the photopic luminosity coefficient at the wavelength of the standard, based upon the JUDD (1951) proposed photopic luminosity coefficients; and the constant represents the combined value of the lumen to watt conversion, the lambert to candle per unit area conversion, and an allowance for the area of the artificial pupil used in the instrument.

The index of spectral sensitivity used was the luminosity coefficient (LC) defined by the relation:

$$\mathrm{LC} = \frac{N_s}{N_c} V_s \tag{2}$$

where N_c = radiance of the comparison wavelength at the apparent brightness match.

By this definition, the luminosity coefficient obtained by the patient at each wavelength should agree with the Judd photopic luminosity coefficient at that wavelength if the spectral sensitivity function is the normal one of foveal cones.

The use of the Judd values, rather than the more standard 1931 CIE values for V_s, affects the values of both E_r and LC we report. A 402 mμ standard was always used in these measurements, so that a single conversion factor adjusts our data to the CIE value of V_s. This factor equals 0·0945, and our values of both E_r and LC are to be multiplied by it to convert our data to the CIE system. We have preferred to use Judd's values rather than the CIE values, because the former are undeniably more accurate at the short wavelengths, which are especially important to the blue-cone mechanism revealed in this paper.

Luminosity coefficients for ten normal subjects of college-age are presented in Fig. 1, together with the 1951 JUDD data. Data were obtained at both a 0·0894 and a 1·52 troland illuminance level. Since the data were found to be identical at the two illuminances, they have been averaged. The normal data represent 164 luminosity measurements at each wavelength. The ordinate scale is the correct scale for our normal data; the Judd coefficients have been adjusted to agree with our data at 550 mμ. There is excellent agreement between the two sets of data at the longer wavelengths. The differences at short wavelengths are probably due to the existence of lesser concentrations of macular xanthophyll in our young subjects than in the subjects involved in Judd's data. This pigment, extracted by WALD (1945) from the macular area of the human retina, is presumed to be located anterior to the photoreceptor cells and hence acts like a colored filter reducing sensitivity at the short end of the spectrum at the wavelengths at which the pigment absorbs. It gives the yellow appearance to the macula lutea, and is known to become more absorptive with increasing age.

Foveal and peripheral dark-adaptation were measured in a recording dark adaptometer constructed along the general lines described by MCLAUGHLIN (1954). The device consists of a pre-adapting field of controllable luminance and duration, and a flashing test light of continuously variable intensity which the patient maintains at a threshold level during dark-adaptation by adjustment of a knob control linked to a circular neutral wedge. For the present studies, the test light subtended 15′ of arc, and was presented intermittently during the entire test period in the following sequence: 2·4 sec on, 1·2 sec off, 2·4 sec on, etc. Viewing could be either monocular or binocular, and natural pupils were used. The experi-

mental sequence consisted of a 900 sec initial period of dark-adaptation to wash out effects of unknown previous adaptation, a period of 500 sec light-adaptation to a luminance of more than 1000 ft-L, and the dark-adaptation test. Fixation was controlled by a diamond configuration of four white lights surrounding the test light for foveal testing and by a single white fixation light 15° from the center of the test light for peripheral testing.

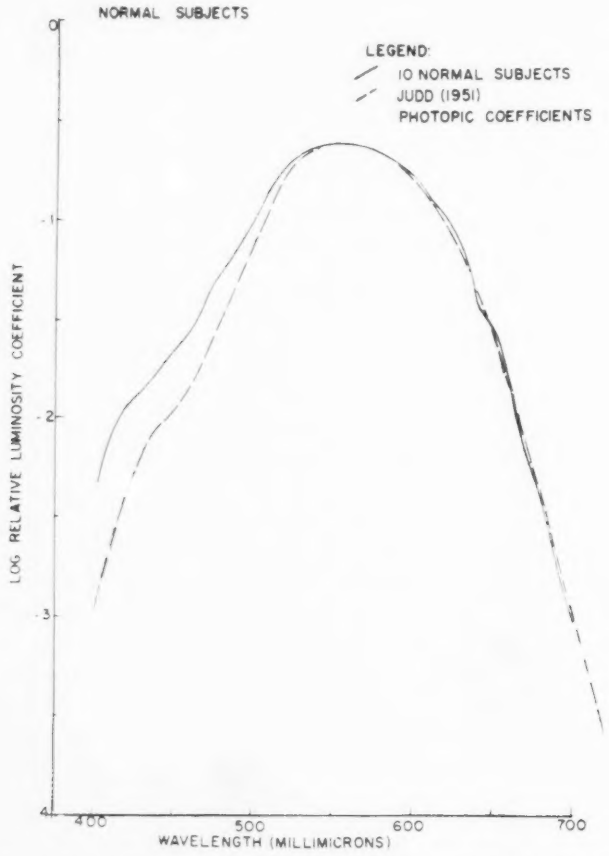

FIG. 1. Average luminosity data for normal subjects compared with the Judd photopic luminosity coefficients. Photopic coefficients adjusted along the ordinate to agree with the data at 550 mμ.

In order to identify the photoreceptor systems responsible for adaptation at different times in the dark, we employed what might be called "spectrophysiological" analysis. This involves measuring dark-adaptation for test stimuli differing in wavelength as did KOHLRAUSCH (1922) and HECHT *et al.* (1948). Quantitative analysis is made convenient by the use of white test stimuli, and colored test stimuli produced by the insertion of colored absorptive filters. The procedure involves determining the effective density of the colored filter from the quantitative change this filter makes in dark-adaptation threshold values. The theoretical density of this filter can be computed for various receptor systems with known

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spectral sensitivities. Comparison of the computed and obtained density values will reveal which of the receptor systems is actually responsible for the dark-adaptation process. BROWN (1956) provided a formal statement of this computational process in another context. SLOAN (1957) was apparently the first to apply this method of analysis to dark-adaptation data. As we shall see, it is a powerful tool which deserves widespread use.

In our use of spectrophysiological analysis, we first measured either the foveal or peripheral dark-adaptation function with a white test stimulus, then repeated the measurement after insertion of a Wratten #47B colored filter in the test light beam. This filter has a peak transmittance at about 430 mμ and a half-width of about $\pm$20 mμ. The pre-adaptation field was white for both the white and blue test light measurements.

We can compute the theoretical density of the #47B filter, assuming a given photoreceptor sensitivity function, and test the extent to which this computed density brings the dark-adaptation threshold values obtained with blue light into agreement with the threshold values obtained originally with white light. We included in our computation of the density of the blue filter measured values of the energy distribution of the test light source and of the spectral transmittance of the various neutral filters and wedges used to adjust the test light to threshold. The density of the #47B filter was computed to be 1·45 for normal rod photoreceptors, represented by the standard CIE Scotopic function, and 2·59 for normal cone photoreceptors, represented by the JUDD (1951) Photopic function. Following SLOAN (1957), we shall refer to these values as the "photopic density" and "scotopic density" of the filter. In adjusting the peripheral dark-adaptation data of normals, we found a considerable variation in the density correction actually needed to bring the blue and white test data into agreement. Presumably this is due to chance variations in the level of the thresholds obtained during different dark-adaptation tests. Peripheral dark-adaptation tests are known to be very unreliable, because we are here measuring the sensitivity of a system near the limit set by quantal fluctuations. Our data may also suffer from differences in the observing methods used by the patients during pre-adaptation. In any event, we have adjusted our blue test data by empirical density corrections designed in each case to bring them into the best possible agreement with the white test data so that we will be able to judge accurately whether more than one class of receptors is involved in a given function. Whenever the density value falls between 1·00 and 1·75, we will attribute the function to rods. The empirical density corrections used throughout the paper will be summarized in the Discussion section so that the reasonableness of this interpretation of the data may be assessed.

Visual acuity was measured at different luminance levels, utilizing a letter chart and projected illumination which could be varied by means of neutral filters. Care was taken to insure that each patient wore an optimal refractive correction. These varied from $-$3·50 to +6·50 diopters of spherical equivalent. The charts utilized involved letters developed by SLOAN *et al.* (1952). Measurements were monocular. The patient hand-held a 2 mm artificial pupil over one eye, the other eye being covered with an opaque patch. He walked toward and away from the chart, until the letter *K* was considered to be just resolvable. Acuity values were computed from the Snellen acuity rating of the letter and the distance from eye to chart. By selection of a suitable size letter on the Sloan Chart, the viewing distances at acuity threshold were kept larger than 5 ft. Three individual measurements were made at a given level of luminance of the chart, then the level was changed and three new settings were made. Measurements were usually made at luminance levels which were reduced in 0·5 log unit steps from highest to lowest, then a second set of measurements were made at levels gradually increased from lowest to highest. Values of retinal illuminance were

computed on the basis of the measured luminance of the test chart and the area of the artificial pupil from the relation:

$$E_r = 10{\cdot}8\ B \tag{3}$$

where E_r = retinal illuminance in trolands; and
B = luminance in ft-L.

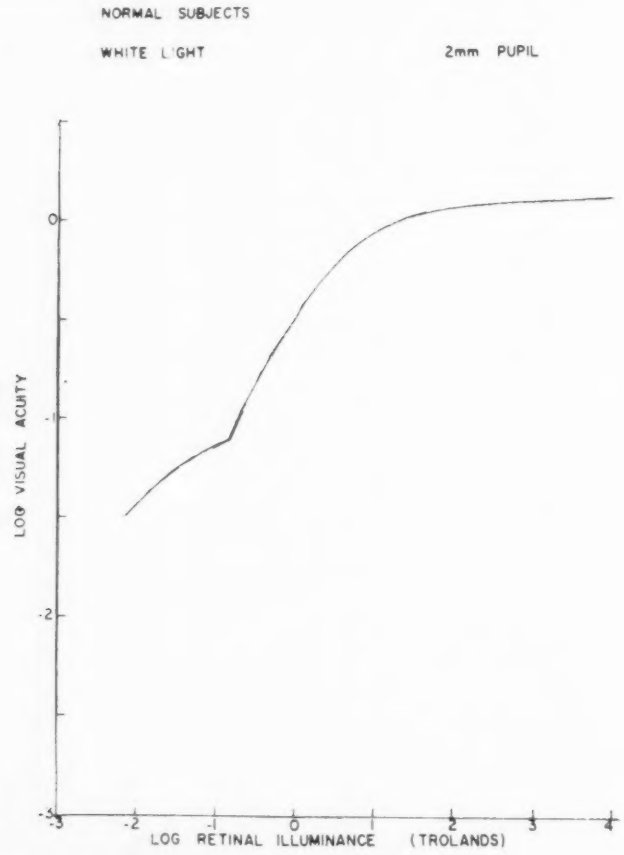

FIG. 2. Average acuity functions of illuminance for normal subjects.

Acuity data (six tests) for two normal subjects of college-age are presented in Fig. 2, utilizing white light illumination of the test chart.[2] The maximum acuity obtained at the highest level of retinal illuminance was 1·20, which corresponds to about twenty in seventeen. The existence of a duplex function presumably reflects the mediation of cone and rod photoreceptors (HECHT, 1937). One method of substantiating this assertion would involve measuring the acuity function again with a colored filter and performing spectrophysiological analysis on the two portions of the acuity curve. As we shall see, this procedure has been followed on our patients. It has not been followed on normal subjects due to complications arising from ocular chromatic aberration. The presence of this aberration means that acuity

[2] Measurements made by Professor Mathew Alpern of The University of Michigan.

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in blue light will be reduced in a manner unrelated to the spectral sensitivity of the functioning receptors. This will introduce particularly great confusion when acuity is measured by varying the viewing distance, as we have done, since the significance of a given amount of chromatic aberration will depend upon the extent to which it may be overcome by changes in accommodation. Chromatic aberration has been shown to have no measurable effect upon the acuity data of our patients due, no doubt, to the low level of their maximum acuity.

It should be pointed out that the presence of chromatic aberration is relatively unimportant even with normals, when applied to dark-adaptation measurements. The test stimulus subtends 15′. The blurring of a test stimulus of this size by an amount to be expected from chromatic aberration in blue light can be shown to have no measurable effect upon the thresholds obtained during dark-adaptation.

MEDICAL FINDINGS

Principal results of the ophthalmological examinations are summarized in Table I for the nine male patients on whom we have extensive data. It appears that classification of these patients would be somewhat difficult on the basis of medical findings alone.

GENETIC FINDINGS

Pedigrees on the six families represented by the nine male patients on whom we have extensive data fall into two general categories. First, there are three pedigrees which appear to be classic examples of a sex-linked recessive transmittance. These are for the L family (EL, GL, RL), the Sc family (HSc) and the St family (HSt). The other pedigrees can all be considered to represent simple recessive transmittance. Summaries of these pedigrees may be obtained from the present authors, with complete records obtainable from The University of Michigan Heredity Clinic.

PSYCHOPHYSICAL FINDINGS

As indicated in the introduction, eight of the patients have been classified on the basis of psychophysical data into three categories of congenital achromatopsia, with consistently different functional characteristics. We will present the psychophysical findings by giving average data for each of these categories.

Category I (Rod Monochromacy): Patients JB, LB, HSt

Color vision measurements. Each patient was examined repeatedly on the spectral comparator. Measurements were made monocularly, each patient selecting the preferred eye. Measurements were always made at two or more levels of retinal illuminance in the range from 0·0738 to 2·08 trolands.

Luminosity measurements obtained with a single standard yield excellent data for the identification of functional monochromacy. The patients were required to match wavelengths as different as 700 and 402 mμ by direct comparison, and were asked whether or not a perfect match was obtained when the radiances were set for a brightness match. The present patients reported perfect matches at all levels of retinal illuminance, so that we may confidently identify them as functional monochromats.

Examination of the individual luminosity data suggested that the data for the three patients were equivalent as were the data obtained at different levels of retinal illuminance.

TABLE I. MEDICAL FINDINGS ON NINE MALE CASES OF CONGENITAL ACHROMATOPSIA

Initials	Fundus appearance			Nystagmus	Photophobia
	Macula	Periphery	Optic disk and vessels		
JB	Pigment clumping; cysts	Retinal atrophy; retinal thinning	White disk with much gliotic reaction; peripapillary atrophy; attenuation of peripheral vessels	No	No
LB	Pigment clumping; cysts	Granular pigmentary change; retinal thinning	Pale and sharply outlined disk; glial tissue piled up on disk margins; attenuation of peripheral vessels	No	No
FB	Minute foveal reflex; slight pigment clumping	Unremarkable	Slight situs inversus of the disk with much vessel branching on disk surface	Gross	Gross
EL	Stippled; minute foveal reflex	Blonde retina; stippled pigment; baring of choroidal vasculature	Enlarged disk	No	No
GL	Minute mottling	Blonde retina; stippled pigment; baring of choroidal vasculature; verrucae	Unremarkable	No	No
RL	Minute stippling; small pigment border; minute foveal reflex	Blonde retina; stippled pigment; baring of peripheral choroid; verrucae	Unremarkable	No, but minor nystagmoid jerking in extremes of gaze	No
HP	Minute foveal reflex	Unremarkable	Unremarkable	Gross (also strabismus)	Gross
HSc	Minute stippling and pigment deficiency	Unremarkable	Unremarkable	No (but strabismus)	Very slight
HSt	Slight swelling; some granularity; minute foveal reflex	Unremarkable	Unremarkable	No	No

The average data (eighteen tests) are presented in Fig. 3, in which the ordinate refers directly to the luminosity coefficients obtained on the patients. The standard CIE Scotopic coefficients have been adjusted for best overall fit. The general agreement between the two curves in Fig. 3 is taken as evidence that the photoreceptors responsible for spectral sensitivity in these patients are rods.

We have no satisfactory way in which to identify the retinal location which the color vision measurements represent. The patients did not have gross nystagmus, and they

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fixated in their normal manner. No large eccentricity of fixation was noted but we had no way to detect small eccentricities of fixation. Our overall analysis suggests that these patients used slightly eccentric fixation, but we have no direct supportive evidence.

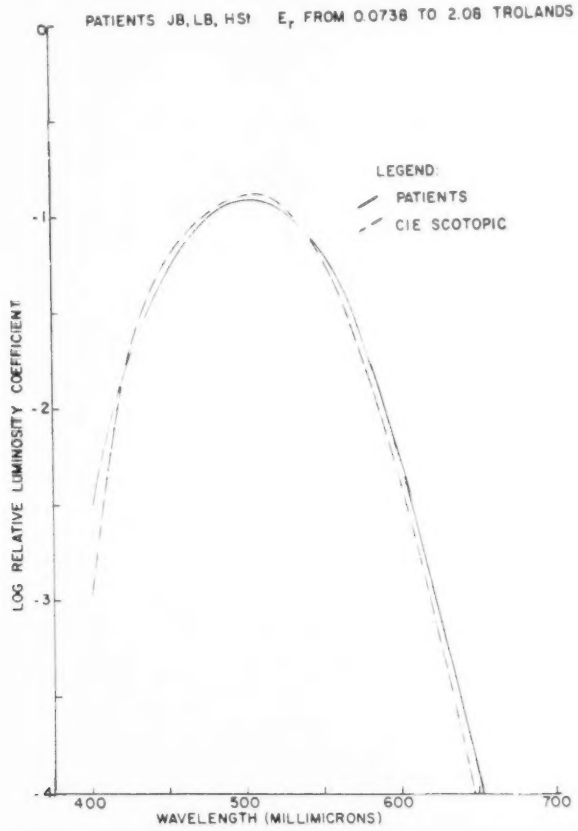

FIG. 3. Average luminosity data for patients JB, LB, and HSt compared with standard scotopic luminosity coefficients. Scotopic coefficients adjusted along the ordinate for best overall agreement with the data.

Dark-adaptation measurements. "Foveal" dark-adaptation measurements were made on each of the three patients, with white and blue test stimuli. Viewing was binocular. The average data (eleven tests) are presented in Fig. 4, in which the ordinate scale refers directly to the white test data. The blue test data have been adjusted along the ordinate by a density correction of 1·07. Since all portions of the two curves agree equally well, we may conclude that the photoreceptors responsible for the entire course of dark-adaptation have the same spectral sensitivity. The density correction of 1·07 is taken to mean that rods are the receptors involved.

Dark-adaptation measurements at a 15° separation from fixation were also made on each of the three patients, with white and blue test stimuli. Viewing was binocular. The average data (eight tests) are presented in Fig. 5, where the ordinate scale refers directly to the white test data. The blue test data have been adjusted by a density correction of 1·33. On

the basis of the overall agreement of the two curves and the value of the adjustment factor, we conclude that rods are responsible for the entire course of dark-adaptation here also.

It is interesting to note that the curves for both white and blue test stimuli obtained in the 15° peripheral location show some evidence of a duplex form. There is lesser evidence of the same result for the foveal data obtained with both white and blue test stimuli. This

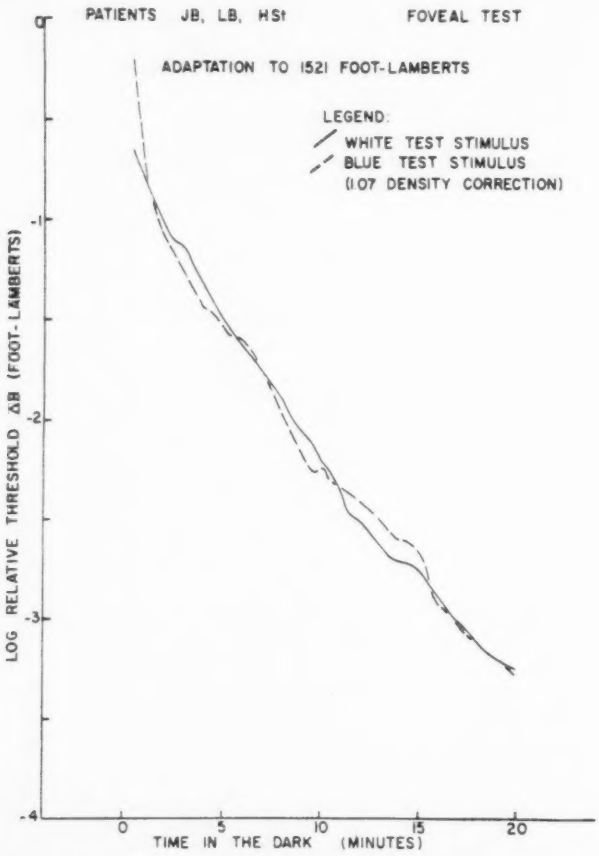

FIG. 4. Average foveal dark-adaptation data for patients JB, LB, and HSt with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·07.

result agrees with SLOAN's finding (1957) that typical achromats have duplex dark-adaptation curves in the fovea and in the periphery, for which both portions have the spectral sensitivity of rods. Although we do not currently have adequate data to substantiate the notion, we have hypothesized that the two rod systems responsible for the duplex dark-adaptation curves differ in the extent to which polysynaptic neural connexions are involved. Thus we postulate that the rapidly adapting rods are functioning through more monosynaptic pathways and the less rapidly adapting rods are functioning through more diffuse neural pathways. Future experiments are planned to test this hypothesis.

Visual acuity measurements. Visual acuity measurements (a total of fifteen) for various illuminances of white light were made for each of the patients. The individual results are

presented in Fig. 6, for comparison with the data for normal subjects previously reported. Individual data are presented because the acuity data constitute the primary basis upon which the patients have been assigned to the three functional categories. Note that each patient shows an acuity function which has a peak value at between 1 and 100 trolands of retinal illuminance, with reduced acuity at both higher and lower illuminances. The reduction of

FIG. 5. Average peripheral dark-adaptation data for patients JB, LB, and HSt with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·33.

acuity at low values of retinal illuminance is, of course, to be expected. The reduction at high levels of illuminance is a peculiarity of this category of patients which is of considerable theoretical interest. These patients do not exhibit photophobia, so that it is not reasonable to suppose that discomfort at high light levels produces blinking which in turn reduces acuity. The reduction in acuity at high levels of illuminance appears to be a fundamental characteristic of the rod receptor system.

It should be emphasized that the levels of retinal illuminance indicated in the acuity and luminosity data are not directly comparable. The troland levels in each case are computed on the basis of the normal photopic curve whereas these patients have a luminosity curve much more like the scotopic curve. Assuming for convenience that the white light used in the acuity measurements has equal energy at each wavelength, we may compute that a

troland of 402 mμ wavelength is effectively twice as bright to our patients as a troland of white light. Taking account of this difference, we may note that our luminosity measurements all represent points on the acuity function at or below the peak value.

Although the precise interpretation of the results may be somewhat ambiguous, we have performed spectrophysiological analysis on the acuity function by measuring visual acuity with blue light as well as white light. Summary data (twelve tests) for the three patients are presented in Fig. 7, for white and blue test light. The abscissa scale values refer directly to

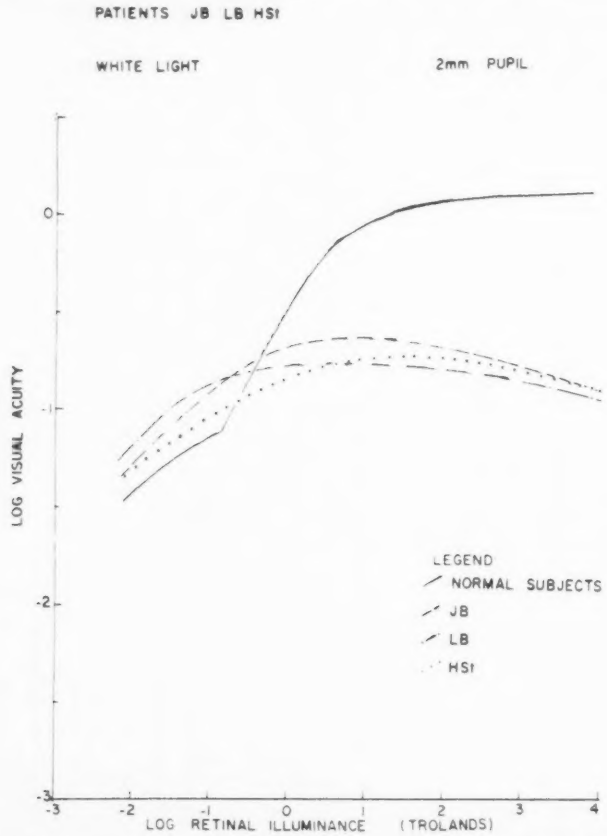

FIG. 6. Individual acuity functions of illuminance for patients JB, LB, and HSt compared with analogous data for normal subjects.

the white light data. The blue light data have been adjusted along the abscissa by a density factor of 1·20. Although there is some difference in shape of the two curves, there is no reason to suppose that two classes of photoreceptors with different spectral sensitivities were involved in the white light data. The density value of 1·20 identifies the receptors as rods. (In this connexion, it should be noted that the scotopic density of the blue filter in the acuity experiment is 1·37 rather than the value of 1·45 reported earlier because of a difference in the wavelength composition of the light sources in the acuity and dark-adaptation experiments. The significance of the precise value of the density correction will be considered further in the Discussion section.)

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Summary. The psychophysical data from luminosity, foveal, and peripheral dark-adaptation, and visual acuity measurements agree in demonstrating that the present patients appear to have only rod receptors and that they have a monochromatic functional system. Thus they may be considered to represent typical achromatopsia or, as we prefer to designate it, rod monochromacy.

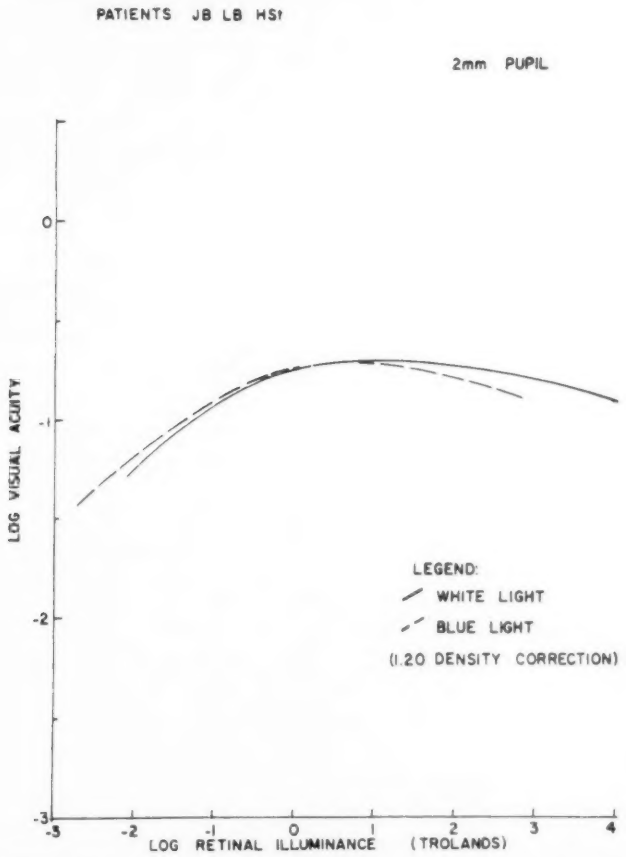

FIG. 7. Average acuity functions of illuminance for patients JB, LB, and HSt with white and blue light. Blue light data adjusted along the abscissa for a density correction of 1·20.

Category II (Blue Monocone Monochromacy): Patients EL, GL, RL

Color vision measurements. Each patient was examined repeatedly on the spectral comparator. As before, measurements were made at different values of the retinal illuminance produced by the initial standard wavelength. The data for the three patients agreed exceptionally well, but there were large and important differences in the data obtained at different illuminance levels.

Average data (seven tests) obtained at an illuminance level of 0·0759 trolands are presented in Fig. 8. The patients were unable to detect hue-differences even between the extreme ends of the spectrum, so that they may be considered functional monochromats at this illuminance level. During these measurements, the patients believed they were using

their normal fixation procedure. Since there is no evidence of eccentric fixation or nystagmus in these patients, this presumably means that fixation fell within the fovea centralis. In the figure, the ordinate values refer directly to the patients' data, the theoretical curves having been adjusted to fit these data at the long wavelengths. It is apparent from the figure that the standard CIE Scotopic curve fits the patients' data at long wavelengths, but departs markedly

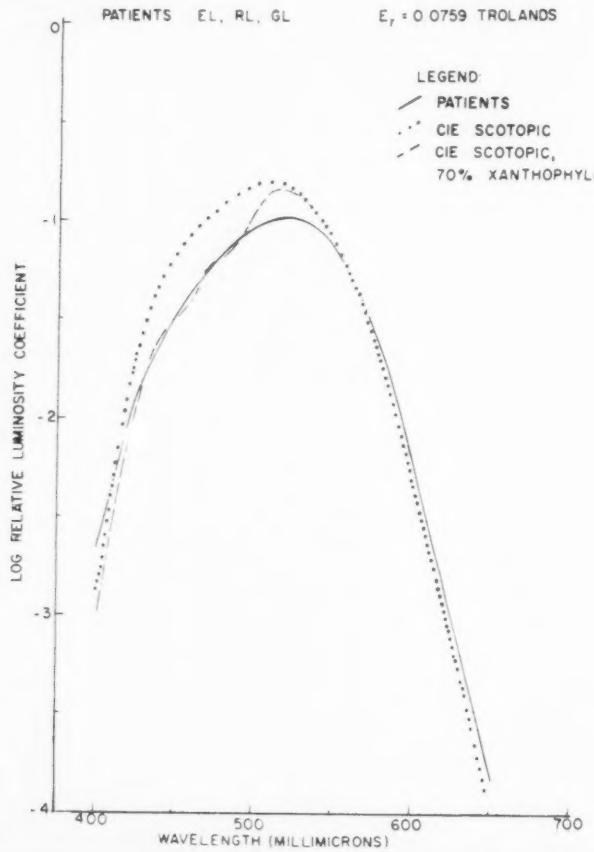

FIG. 8. Average luminosity data for patients EL, GL, and RL compared with standard scotopic luminosity coefficients, and with these coefficients modified by absorption of a 70 per cent concentration of macular xanthophyll. Scotopic coefficients adjusted along the ordinate for best agreement with the long wavelength data.

in the range from 410 to 540 mμ. It occurred to us that this discrepancy between the data and the standard scotopic curve might be due to the presence of macular xanthophyll, the yellow pigment presumed to overlay the macular receptors. Use was made of the absorption spectrum of this substance reported by WALD (1945). It was found that a concentration 70 per cent of that reported by Wald provided the best fit to our data. The xanthophyll-corrected CIE Scotopic function is shown in the figure to provide a much better fit to our data than does the standard scotopic function. This presumably means that the spectral sensitivity of our patients is due to rod receptors located near the approximate center of the macular region where the concentration of macular xanthophyll is high. It is, of course, of

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considerable theoretical interest that we have found this evidence of functional rods in what is presumably the fovea centralis. It is also of considerable interest that these data support the contention that macular xanthophyll does indeed overlay the photoreceptors in the macular retina.

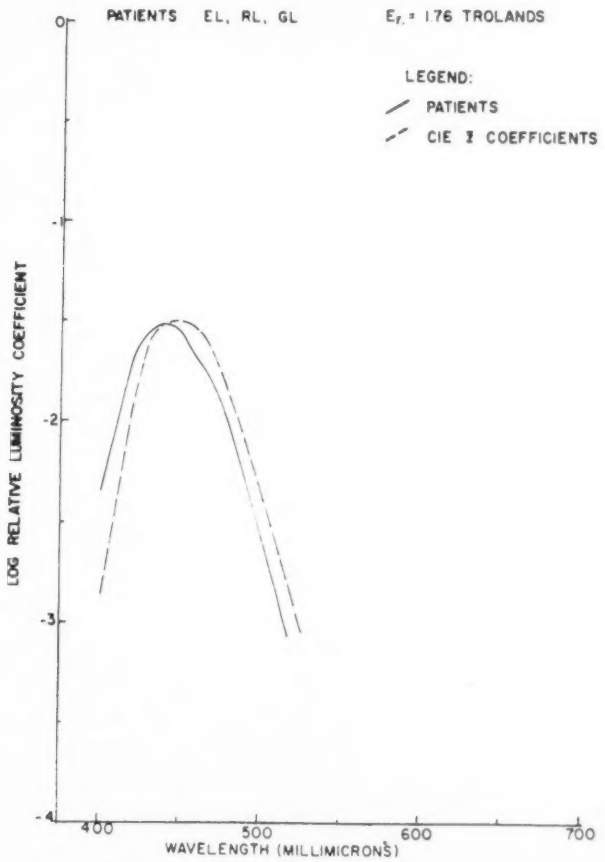

FIG. 9. Average luminosity data for patients EL, GL, and RL compared with the standard $\bar{z}$ coefficients derived from color mixture data. $\bar{z}$ coefficients adjusted along the ordinate for best overall agreement with the data.

We can presumably identify our patients at this illuminance as *foveal* rod monochromats.

Precisely similar measurements were made on each patient at a retinal illuminance level of 1·76 trolands, with the results of eleven tests shown in Fig. 9. During these measurements, the patients were again unable to detect hue-differences between the 402 mμ standard and any other wavelength, so that we may consider them functionally monochromatic. The luminosity function is, of course, enormously different from the one found at the lower illuminance level. The extent of difference may be obscured by the use of logarithms. At 520 mμ, for example, the luminosity coefficients differ by more than a hundred to one! The luminosity curve presented in Fig. 9 is apparently the first ever obtained with a sensitivity maximum less than 500 mμ, and must be considered a real discovery.

The presumed significance of the luminosity curve obtained ot the 1·76 troland level may be understood by reference to Fig. 9 where the CIE $\bar{z}$ function is presented in comparison with the luminosity data for our patients. The general agreement between the curves is good. It was on this basis that we earlier (BLACKWELL, H. R. and BLACKWELL, O. M., 1957) classified these patients as blue monocone monochromats. Theoretical aspects of blue cone luminosity have been considered elsewhere (BLACKWELL, H. R. and BLACKWELL, O. M., 1959).

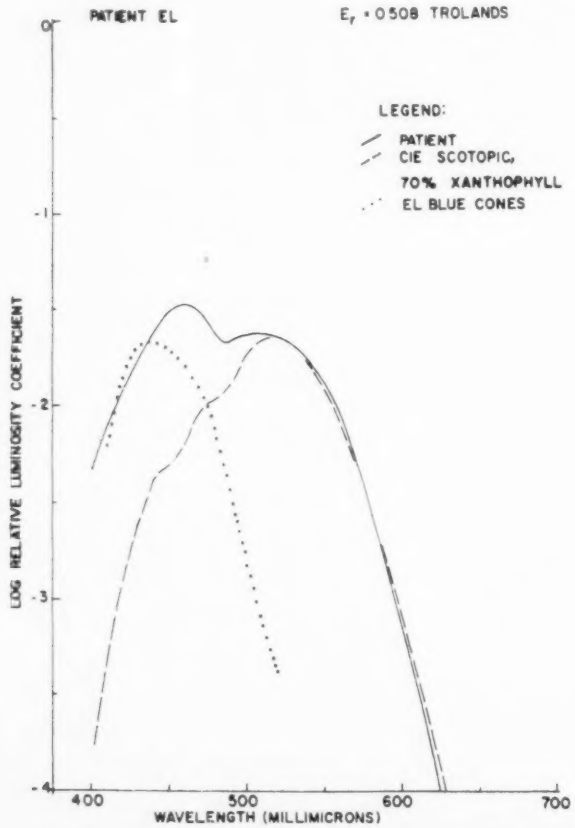

FIG. 10. Individual luminosity data for patient EL compared with standard scotopic luminosity coefficients modified by absorption of a 70 per cent concentration of macular xanthophyll, and with this patient's blue cone luminosity coefficients. Coefficients adjusted along the ordinate so that scotopic coefficients agree best with long wavelength data, and so that blue cone coefficients agree best with short wavelength data.

Luminosity measurements were made on each patient at levels of retinal illuminance intermediate between the two levels reported above. Each patient showed evidence of spectral sensitivity representing a mixture of blue cone and foveal rod systems, and each patient showed dichromatic color-discrimination. The curves obtained on each patient differ sufficiently so that average data would be misleading. The average of two tests at an illuminance of 0·508 trolands for patient EL are presented in Fig. 10 to illustrate the general nature of these data. The luminosity curve has two peaks. It was found that the patient

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could make color-discriminations between wavelengths shorter than 440 and wavelengths longer than 530 mμ, calling the short wavelengths "blue" and the long wavelengths "yellow". There was a neutral zone between about 450 and 510 mμ.

These results may be understood in terms of the construction in Fig. 10. Here the CIE Scotopic curve, corrected for a 70 per cent concentration of macular xanthophyll, has been adjusted to fit the red end of the luminosity curve, and the patient's own blue cone curve obtained at the 1·76 troland level has been adjusted to fit the blue end of the luminosity

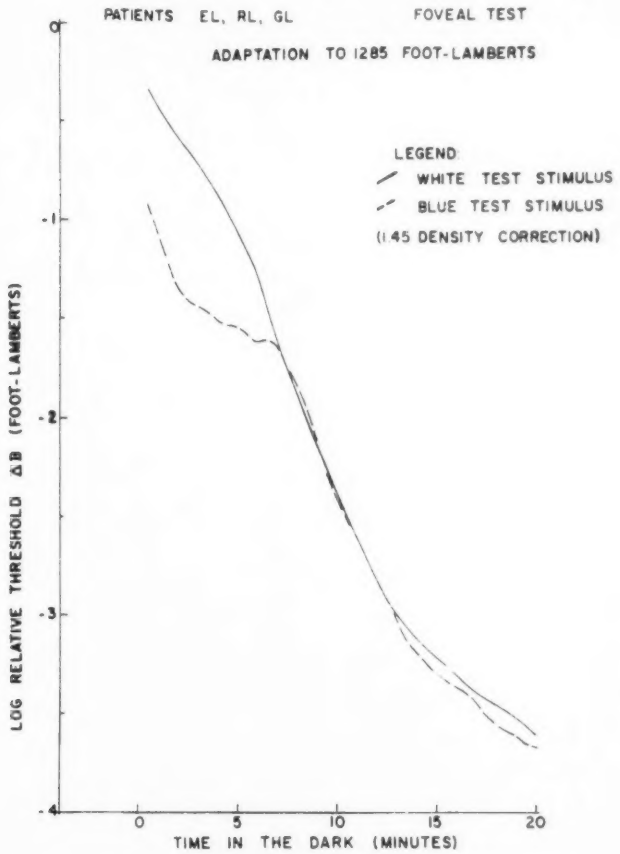

FIG. 11. Average foveal dark-adaptation data for patients EL, GL, and RL with white and blue test stimuli. Blue test data adjusted along the ordinate for density correction of 1·45.

curve. If we assume that blue cones and foveal rods are both operating at this illuminance level, this adjustment procedure presumably determines their relative sensitivities. The fact that the patient can discriminate short from longer wavelengths presumably means that color-discrimination can be based upon differential stimulation of blue cones and rods. The presence of the neutral zone presumably means that the degree of stimulation of the blue cones and rods in this region is too nearly similar to provide a basis for discrimination.

The construction suggests that luminosity summation can occur between blue cones and rods, since the luminosity data fall consistently above the blue cone or rod curves at all

wavelengths within the neutral zone. The extent of summation is seen to be greatest at the precise wavelength at which the blue cone and rod curves cross, at which the sensitivity of the two systems are equal, and is virtually a total summation.

The color vision measurements are taken to mean that these patients have blue cones and rods in the fovea centralis. At low illuminance levels, the foveal rods dominate spectral sensitivity and the patients function as rod monochromats. At high illuminance levels, the

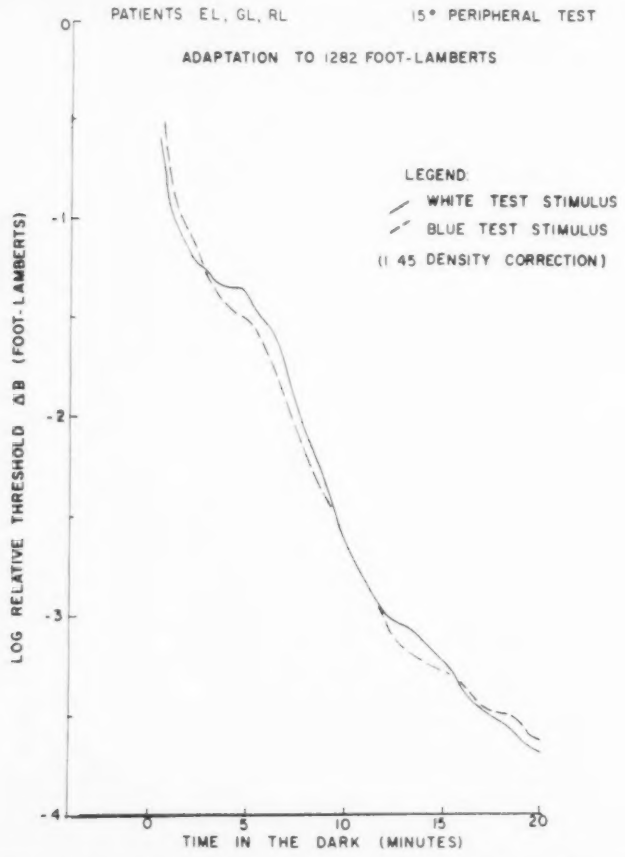

FIG. 12. Average peripheral dark-adaptation data for patients EL, GL, and RL with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·45.

blue cones dominate spectral sensitivity and the patients function as blue monocone monochromats. At intermediate levels of illuminance where the two receptor systems have more nearly equal sensitivity, the patients are blue cone–rod dichromats.

Dark-adaptation measurements. Foveal dark-adaptation measurements were made on each of the three patients, with the average results of six tests shown in Fig. 11. Viewing was binocular. The ordinate scale refers directly to the white test data. The blue test data have been adjusted by a density factor of 1·45. The two curves agree quite well after 7 min in the dark but the blue test data fall far below the white data curve during the early minutes of dark-adaptation. This demonstrates that the foveal dark-adaptation process is not mediated

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by photoreceptors all of which have the same spectral sensitivity. The density factor used in adjusting the data establishes that the later phase of dark-adaptation is mediated by rods. The early phase of dark-adaptation is mediated by receptors with greater blue sensitivity than rods. It was considered likely that the blue cones, whose sensitivity is shown in Fig. 9, were the receptors involved. By adjusting the blue test data for a density of 0·53, the theoretical density of the blue filter for blue cones, we find that the blue cones are primarily

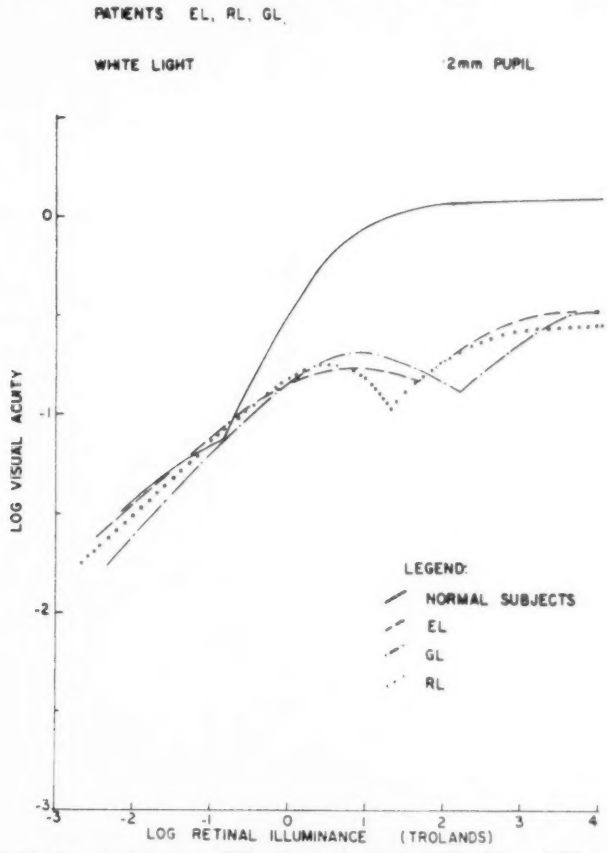

FIG. 13. Individual acuity functions of illuminance for patients EL, GL, and RL compared with analogous data for normal subjects.

responsible for early dark-adaptation and that the rods become increasingly dominant as dark-adaptation continues, until they alone are involved. (It should be noted that the scotopic density of the blue filter will be greater for the foveal rod than for the peripheral rod system. Consideration of this difference will be delayed until the Discussion section.)

Dark-adaptation data for a 15° peripheral location were obtained on each patient, with the average results of six tests shown in Fig. 12. Viewing was binocular. As usual, the ordinate scale refers directly to the white test data. The blue test data have been adjusted again by a density factor of 1·45. On the basis of the overall agreement between the curves, and the value of the density adjustment factor, we may conclude that rods are responsible for the entire course of dark-adaptation. There is strong evidence that there are two classes of rods, the rapidly and the more slowly adapting rods.

The dark-adaptation data thus confirm the general conclusion reached from the color vision measurements, that there are functioning blue cones and rods in the fovea of these patients. These receptors are separated during dark-adaptation because the blue cones dark adapt more quickly than do the rods. There is no evidence that a significant number of functioning blue cones exist at a retinal location 15° from the fovea.

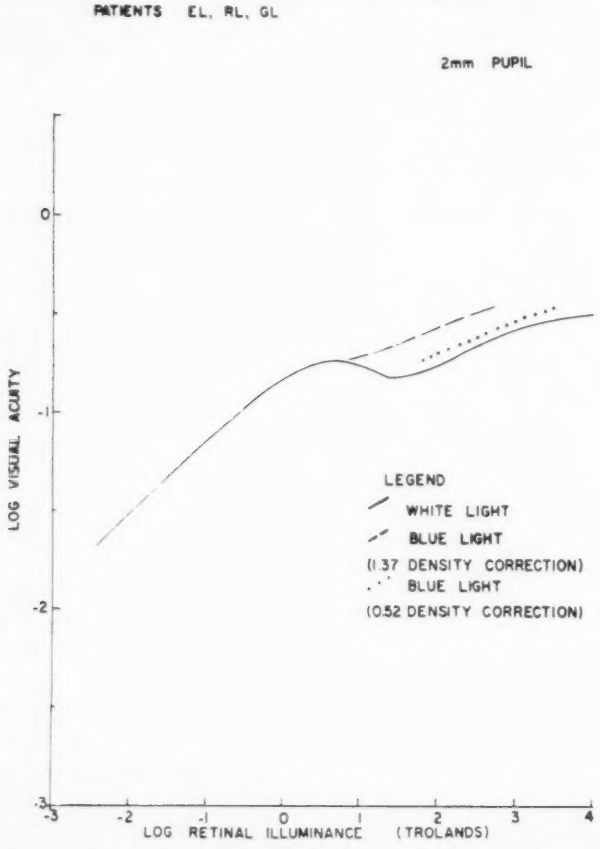

FIG. 14. Average acuity functions of illuminance for patients EL, GL, and RL with white and blue light. Blue light data adjusted along the abscissa for density corrections of 1·37 (rods) and 0·52 (blue cones).

Visual acuity measurements. Visual acuity measurements for various luminances of white light were made for each patient, with the results (a total of nine tests) presented in Fig. 13.[3] The data for each patient exhibit a deep cusp in acuity occurring at an illuminance level somewhere between 20 and 200 trolands. The duplex nature of these curves suggested that two receptor systems were involved. Accordingly, we measured acuity on these patients with the identical technique used for the white light measurements except that a #47B filter was used. Average data for white and blue light (nine tests each) are presented in Fig. 14. The abscissa scale refers directly to the white light data. The blue light data have been adjusted on the illuminance scale by a density of 1·37, which is the precise density of the

[3] Measurements made by Professor Mathew Alpern of The University of Michigan.

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blue filter computed from the standard scotopic function for use with acuity data. This adjustment brings the white and blue light data into such good agreement at low illuminance values that only the white light curve shows. It is apparent that rods are responsible for acuity at low illuminance, but that a more blue-sensitive receptor system is responsible for acuity at high illuminance.

We tested the assumption that blue cones were responsible for the blue light acuity data at high luminance which departed from the white light data, by adjusting these data separately by a density factor of 0·52. This value represents the theoretical density of the blue filter for the blue cones in the acuity experiment. (This value differs slightly from the value of 0·53 given previously as the theoretical blue cone density of this filter, due to differences in the spectral composition of light in the two cases.) The data now agree more closely with the white light data than before. This agreement demonstrates that blue cones are probably responsible for the acuity of these patients at the higher illuminances.

Interestingly enough, however, even after adjustment by the 0·52 density, the blue light data fall at consistently higher values of acuity than the white light data. It seems reasonable to suppose that the rods exert an inhibitory influence upon the blue cones at high values of illuminance which shows up with white light stimuli but is minimized by the use of blue light. This might come about through the use of common synapses by the two classes of receptors, or it might result from excessive neural noise produced by the over-stimulated rods. The second hypothesis has some indirect support. When required to read under the blue light produced by either the #47B filter or by a mercury vapor lamp, the patients each reported the absence of "snow" which they customarily saw obscuring dark letters at high levels of white light.

It is also possible that the blue cones inhibit the rods at intermediate illuminance levels. This is suggested by the more rapid decline of the rod portion of the white light acuity curve with increased illuminance for these patients than was found for the patients in Category I, who presumably have only rods. (Compare Figs. 6 and 13.)

It is interesting that, whereas the white light data show a cusp at intermediate levels, the blue light data (dashed curve in Fig. 14) show only a plateau. The absence of a cusp in the blue light data does not necessarily demonstrate either cone–rod or rod–cone inhibition. It could be assumed merely that blue light gave the blue cones a relative advantage at illuminance levels at which the rods show an acuity decline in white light. With this advantage, the blue cones mediate acuity at these levels. Since there is no evidence that blue cones alone produce a cusp in the acuity curve, their preempting the acuity function at a lower illuminance level would be presumed to eliminate the cusp from the acuity data obtained with blue light.

It should be noted that acuity in blue light might be expected to be less than in white light due to the effects of uncorrected ocular chromatic aberration. In order to evaluate the possible significance of this effect, we obtained complete acuity functions on our patients with blue light, with a minus ophthalmic lens to correct for the myopia to be expected in blue light. The lens was fitted individually to each patient by subjective techniques, working at a 20 ft distance. A −1 diopter lens was used with patients EL and RL, and a −1·50 diopter lens was used for patient GL. The acuity functions obtained with the extra minus lenses were found to be virtually identical with the acuity functions obtained with the patients' regular ophthalmic corrections. These results indicate that uncorrected ocular chromatic aberration apparently did not have a significant effect upon the acuity data obtained with blue light.

In comparing the acuity and luminosity data, it is necessary to take account of the differences in the effective illuminance of white and blue light due to the differences between the luminosity curves for our patients and the photopic curve used to compute the troland levels. As noted earlier, the effective illuminance of the 402 mμ luminosity standard will be about two times greater for rod receptors than the original calculations suggest. The effective illuminance of 402 mμ will be more than forty times greater for the blue cone receptors than calculated. Applying these corrections to the troland levels used for luminosity

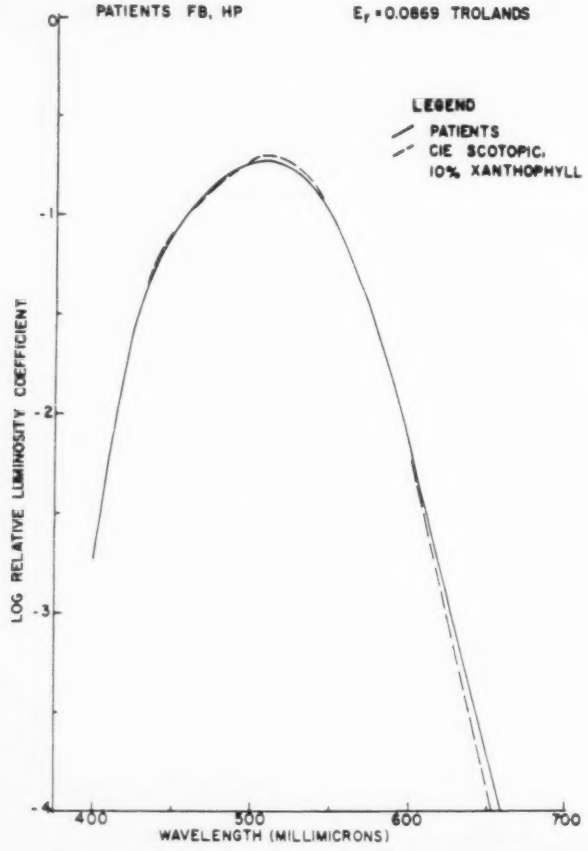

FIG. 15. Average luminosity data for patients FB and HP compared with standard scotopic luminosity coefficients modified by absorption of a 10 per cent concentration of macular xanthophyll. Scotopic coefficients adjusted along the ordinate for best overall agreement with the data.

measurements, we note that the lower illuminance, at which only rods were functioning, corresponds to a value well down on the lower segment of the acuity curve. The upper illuminance, at which blue cones were functioning in luminosity, falls toward the lower part of the upper segment of the acuity curve.

Summary. In summary, the luminosity, the foveal dark-adaptation, and the acuity data agree in revealing the existence of both functional blue cones and rods in these patients. When both systems are of nearly equal sensitivity, the patients possess a dichromatic color

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system. When either the blue cones or the rods are of much greater sensitivity, the patients exhibit monochromacy. There is clear evidence of blue cone–rod summation in the luminosity function. There is some evidence of inhibition both of rods upon blue cones and of blue cones upon rods in the acuity function.

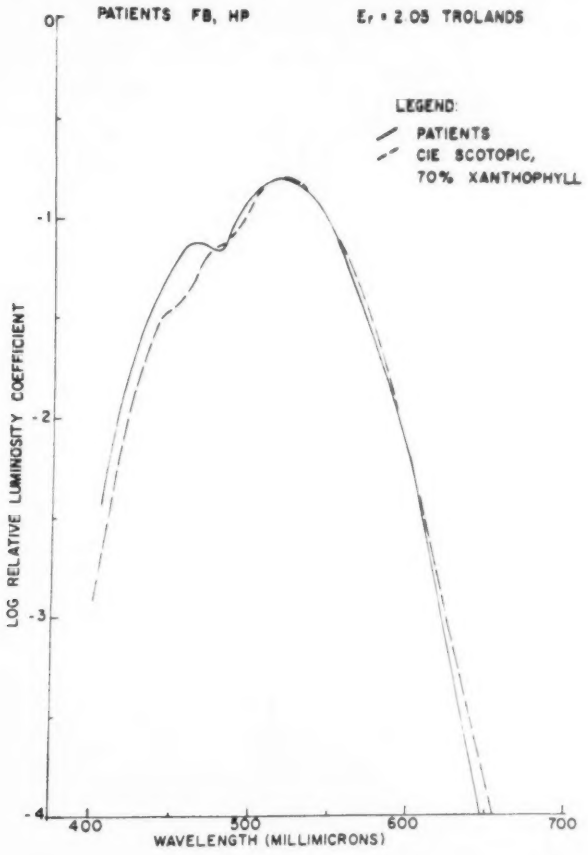

FIG. 16. Average luminosity data for patients FB and HP compared with standard scotopic luminosity coefficients modified by absorption of a 70 per cent concentration of macular xanthophyll. Scotopic coefficients adjusted along the ordinate for best agreement with the long wavelength data.

Category III (Intermediates): Patients FB, HP

Color vision measurements. Each patient was examined on the spectral comparator at different levels of retinal illuminance, as before. Average data (two tests) obtained at an illuminance level of 0·0869 trolands are presented in Fig. 15. The patients obtained perfect matches with all wavelength combinations, so may be classified as monochromats under these circumstances. In the figure, the ordinate values refer directly to the patients' data, the theoretical curve having been adjusted to fit these data. The curve best fit to the data is the standard CIE Scotopic curve, modified by assuming a 10 per cent concentration of macular xanthophyll. The data clearly do not fit the 70 per cent xanthophyll curve fitted to the data

obtained by the Category II patients at this level of retinal illuminance. They may be fitted reasonably well by the standard CIE Scotopic curve fitted to the data obtained by the Category I patients at all illuminance levels.

Average data (four tests) obtained at an illuminance level of 2·05 trolands are presented in Fig. 16. Here also the patients obtained perfect matches all across the spectrum, thus exhibiting a monochromatic functional system. The ordinate refers directly to the patients' data, the theoretical curve having been adjusted for best fit to the data at long wavelengths.

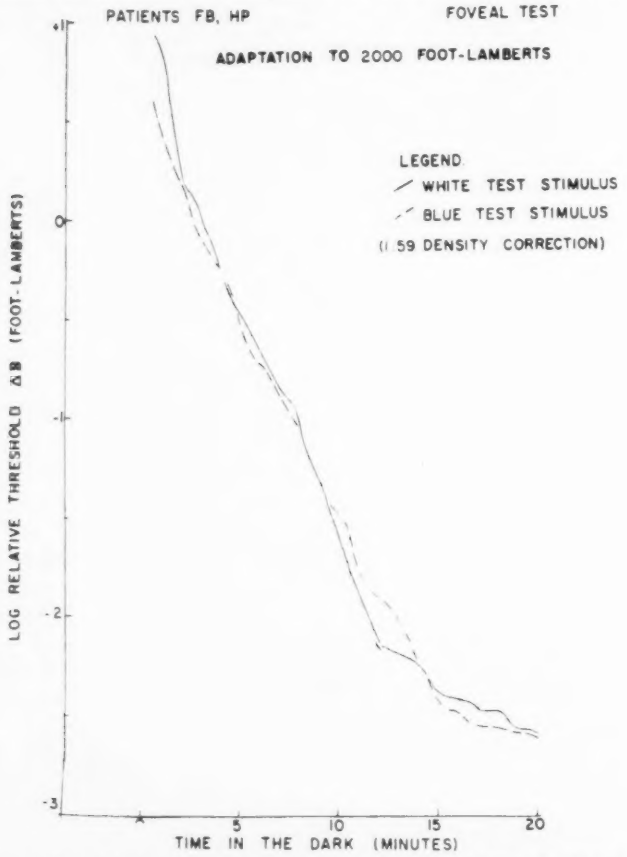

FIG. 17. Average foveal dark-adaptation data for patients FB and HP with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·59.

These data cannot be adequately fitted with either the standard CIE Scotopic curve, or this curve modified by a 10 per cent concentration of xanthophyll. The CIE Scotopic curve with 70 per cent concentration of macular xanthophyll fits the data very well at wavelengths longer than 475 mμ. At shorter wavelengths, the patients exhibit a small but consistent tendency for greater blue sensitivity than is indicated by the theoretical curve. These results suggest that the patients utilized more nearly foveal fixation in making the measurements at 2·05 trolands than in making the otherwise identical measurements at the lower level of retinal illuminance, thus bringing a greater concentration of xanthophyll into play. An indication of blue cone function has been found, presumably partly because of the relative

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advantage these receptors have at the higher illuminance level and possibly also because of the more central locus of fixation presumably used. There were, however, an insufficient number of blue cones compared to rods to provide the patients with a dichromatic functional system.

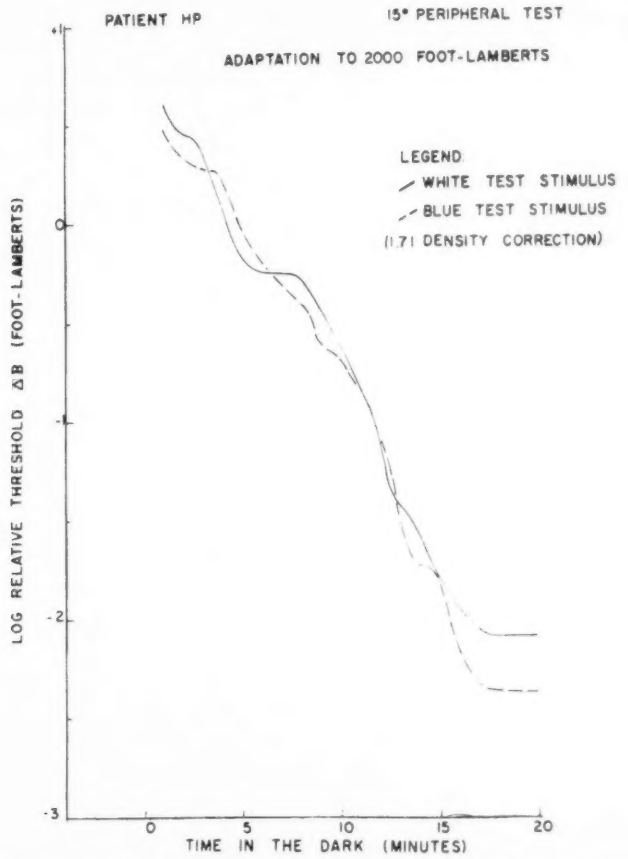

FIG. 18. Individual peripheral dark-adaptation data for patient HP with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·71.

Dark-adaptation measurements. Foveal dark-adaptation measurements were made on each patient, with the average results (four tests) shown in Fig. 17. Viewing was monocular. The ordinate scale refers directly to the white test data. The blue test data have been adjusted by a density value of 1·59. The two curves agree reasonably well overall, indicating that rods are probably responsible for the entire course of dark-adaptation. There is a consistent tendency for the blue data to fall below the white data during the first two minutes of dark-adaptation, but this may be within the error limits of the two curves. If a real effect, it is consistent with the view that a few blue cones are involved in the earliest portion of the foveal dark-adaptation process.

Dark-adaptation data for a 15° peripheral location were obtained on patient HP only, with the results of two tests shown in Fig. 18. Viewing was monocular. The ordinate refers directly to the white light data, the blue data having been adjusted by a density value of 1·71.

The curves seem to agree in shape overall, indicating that only rod receptors are involved in peripheral dark-adaptation. Two segments are obvious in the dark-adaptation curves, indicating again the existence of two kinds of rods.

Visual acuity measurements. Visual acuity measurements for various luminances of white light were made for each patient, with the results of nine tests presented in Fig. 19. The acuity data for each patient show a small but definite cusp at about 1000 trolands of retinal illuminance. It is apparent that these patients are intermediary between the Category I and II patients in terms of their acuity function. Presumably, the duplex nature of these curves

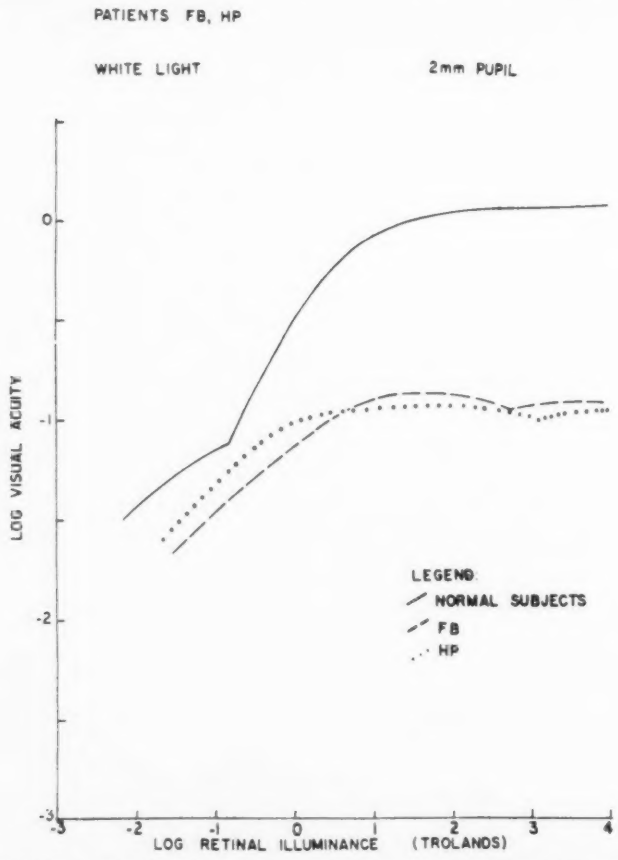

FIG. 19. Individual acuity functions of illuminance for patients FB and HP compared with analogous data for normal subjects.

reflect the existence of two receptors. On the basis of the data for the other patients, it is reasonable to suppose that rods are responsible for acuity at low illuminance, with blue cones responsible for acuity at high illuminances.

Acuity data were also obtained with blue light, the average data (nine tests) being presented in Fig. 20. The abscissa refers directly to the white light data. The blue light data have been adjusted along the abscissa by a 1·70 density value. The blue and white light data agree well over their entire range, suggesting that rods are responsible for the lower segment

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of the acuity curve. There was no way to obtain sufficiently high levels of illuminance through the blue filter to test critically whether or not the high luminance segment represents the activity of rod or blue cone receptors.

Summary. The luminosity and acuity, and perhaps the foveal dark-adaptation data, agree in demonstrating that these patients possess rods and a few blue cones, although an insufficient number apparently to permit dichromatic color-discrimination. There is some

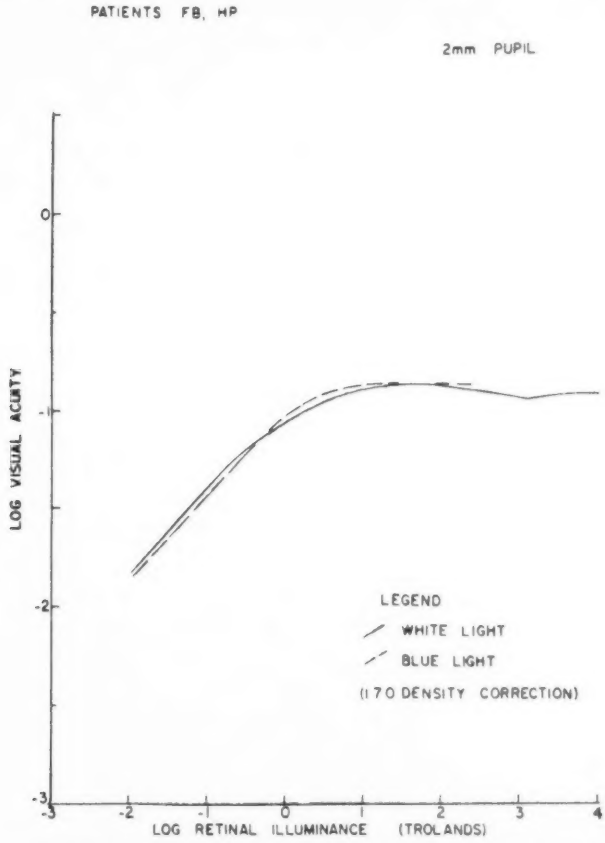

FIG. 20. Average acuity functions of illuminance for patients FB and HP with white and blue light. Blue light data adjusted along the abscissa for a density correction of 1·70.

evidence that the patients direct their fixation nearer to the fovea centralis at higher illuminances. It is to be noted that these patients, alone of any reported thus far, have gross nystagmus. As we shall see, it is our contention that this is the important basis of the difference between these and the Category I patients.

Affected Siblings of Patients in Categories I and III: Patients RB, JP, DSt, JSt

Four patients affected with congenital achromatopsia have been examined who are siblings of patients already reported as members of Categories I and III. These patients were all quite young and could not be subjected to the various quantitative analyses which we have reported in the foregoing sections. As was mentioned earlier, the basic criterion used

to classify the patients was the shape of the acuity function of illuminance. The extent of difference among the acuity functions may be judged from Fig. 21, in which average data for the three categories are compared with each other and with data for normal subjects. As noted earlier, the Category I data are presumed to represent functioning rods alone, the Category III data represent rods and a few blue cones, and the Category II data represent rods and substantial numbers of blue cones. At this point, we are interested only in demonstrating that the acuity functions are differentiable for the three categories of patients.

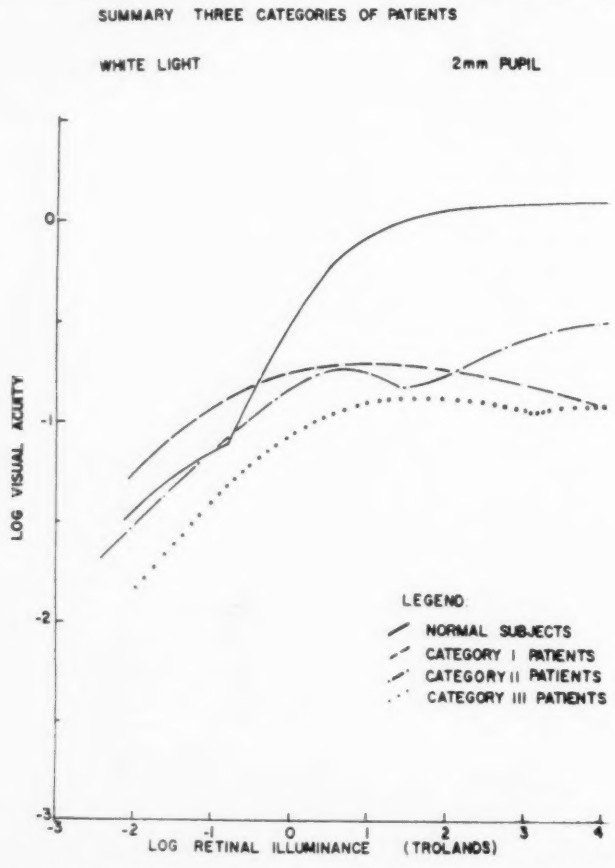

FIG. 21. Average acuity functions of illuminance for the three categories of patients compared with analogous data for normal subjects.

Patient RB. This patient was age six at the time of examination. He was able to take the F-M Test and obtained a pattern of errors similar to those found (but not reported) for the patients in Categories I and III. He did not exhibit manifest gross nystagmus and so was able to take the acuity test with artificial pupil in the usual way. Two data points were obtained, which are presented in Fig. 22 together with the average data for the Category I and III patients. It seems clear that the patient may be classified in Category I on the basis of the acuity function, the category in which his brothers JB and LB were placed.

Patient JP. This patient was age ten at the time of measurement. Only color vision test data are available, on the basis of which he is classified as either a Category I or III patient.

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Patients DSt and JSt. These patients were age twelve and nine respectively at the time of examination. Both exhibited gross nystagmus. Both took the F-M Test and each obtained a pattern of errors similar to those of the patients in Categories I and III. Acuity functions of luminance were measured but it was not possible for these patients to use the artificial pupil. The measurements were made with natural pupils, therefore, and binocular vision was allowed. Subsequently, it was possible to obtain comparable acuity data for patients JB and LB, who, together with HSt, the present patients' older brother, constituted the members of

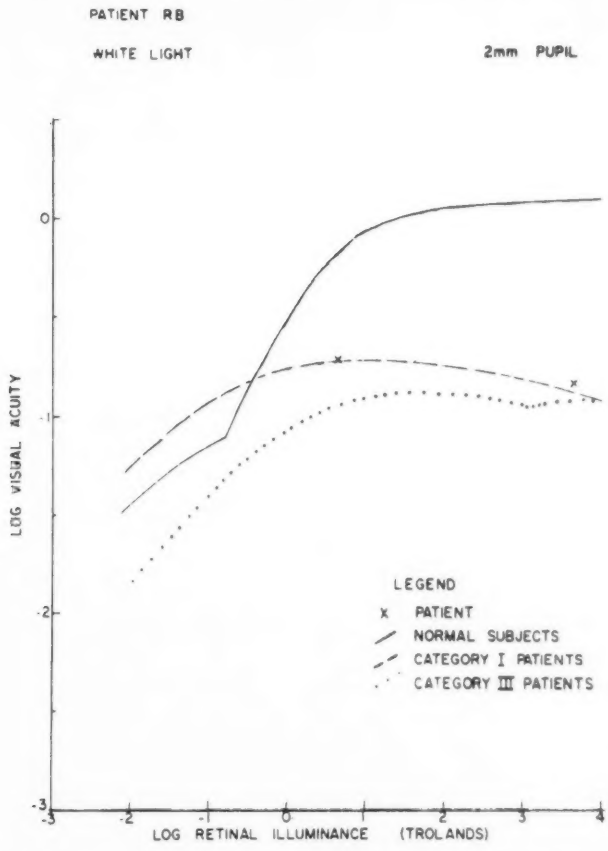

FIG. 22. Individual acuity data for patient RB compared with analogous data for Category I and III patients, and for normal subjects.

Category I. The acuity data for DSt and JSt are presented in Fig. 23, compared with the data from the two Category I patients. We conclude that there is a difference here, analogous to the difference found previously between the Category I and III patients when acuity was measured with the artificial pupil. It would appear from these data that patients DSt and JSt belong to Category III rather than to Category I.

The acuity data, and the presence of nystagmus, agree in classifying DSt and JSt in Category III rather than Category I. These patients are siblings of patient HSt who belongs to Category I, and who does not exhibit nystagmus. It is suggested that the only difference

between the patients in Categories I and III may be the presence or absence of nystagmus. We shall return to this point subsequently.

Patient HSC

This patient was a student at The University of Michigan whom we discovered on the basis of color vision tests administered during a Hospital Open House. He was unusually intelligent and interested in our studies, and cooperated fully with us on a great many occasions. As we shall see, this patient may be identified with each and every one of our three categories, depending upon the precise measurement conditions.

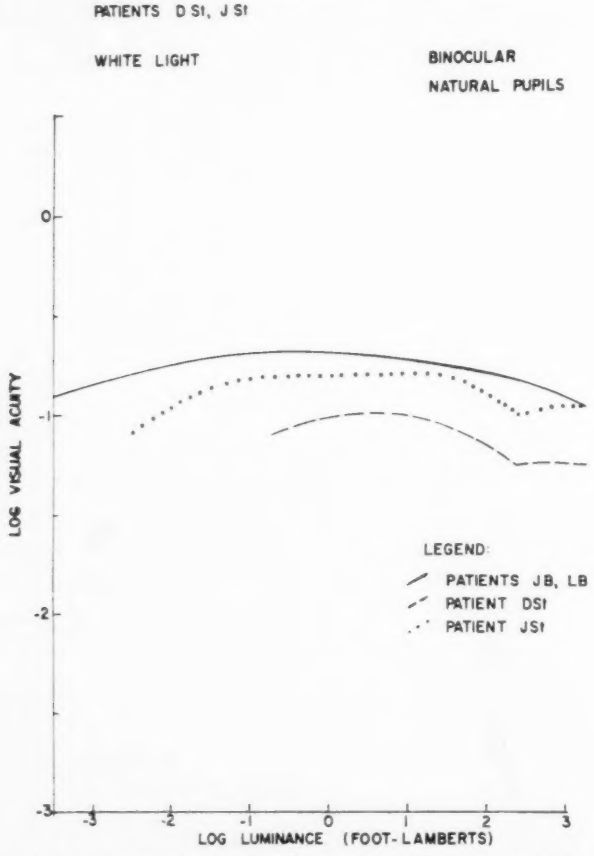

FIG. 23. Individual acuity functions of illuminance for patients DSt and JSt compared with analogous average data for patients JB and LB.

Color vision measurements. Initially, luminosity curves were obtained on the left eye of the patient. The data (five tests) obtained at 0·0751 trolands are presented in Fig. 24. The patient was unable to make consistent color-discriminations between spectral pairs, and hence could presumably be classified as a functional monochromat. The luminosity data in the figure are fitted adequately by the CIE Scotopic curve, modified by a 70 per cent concentration of macular xanthophyll. They cannot be fitted by the standard Scotopic curve. The resemblance of these data to the corresponding data for the Category II patients,

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presented in Fig. 8, is really excellent. We can presumably conclude that, at this illuminance level, the patient is a foveal rod monochromat as were the Category II patients.

Luminosity data (three tests) for this patient at 1·68 trolands are presented in Fig. 25, together with the corresponding data for the Category II patients originally presented in Fig. 9. The patient was unable to make hue-discriminations between any combinations of wavelengths, and so was a functional monochromat. The agreement between his data and the data of the Category II patients is sufficiently good so that we may confidently classify the patient as a blue monocone monochromat.

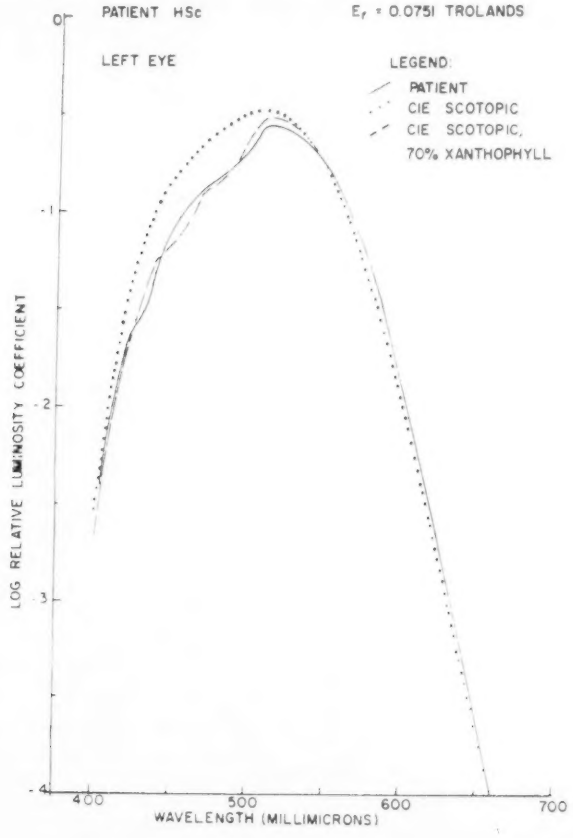

FIG. 24. Individual luminosity data for the left eye of patient HSc compared with standard scotopic luminosity coefficients, and with these coefficients modified by absorption of a 70 per cent concentration of macular xanthophyll. Scotopic coefficients adjusted along the ordinate for best agreement with the long wavelength data.

Luminosity data obtained at intermediate illuminance levels exhibited the general mixed form shown for patient EL in Fig. 10. Under these conditions, the present patient also exhibited a dichromatic color vision system based upon blue cones and rods.

Foveal dark-adaptation data (two tests) for the patient are presented in Fig. 26, for white and blue test stimuli. Viewing was monocular. The ordinate scale refers to the white test data; the blue test data have been adjusted by a density value of 1·45. In spite of the

erratic data, it is clear that dark-adaptation following 8 min in the dark is mediated by a single class of receptors having the spectral sensitivity of rods. During the first few minutes in the dark there is fairly clear evidence of the existence of blue cone receptors since the blue test data fall consistently below the white test data. It is confirmatory that the patient reported that the test stimulus looked blue during the first 3 min of dark-adaptation and colorless thereafter. These data are not as convincing, however, as the data on the Category II patients, presented in Fig. 11.

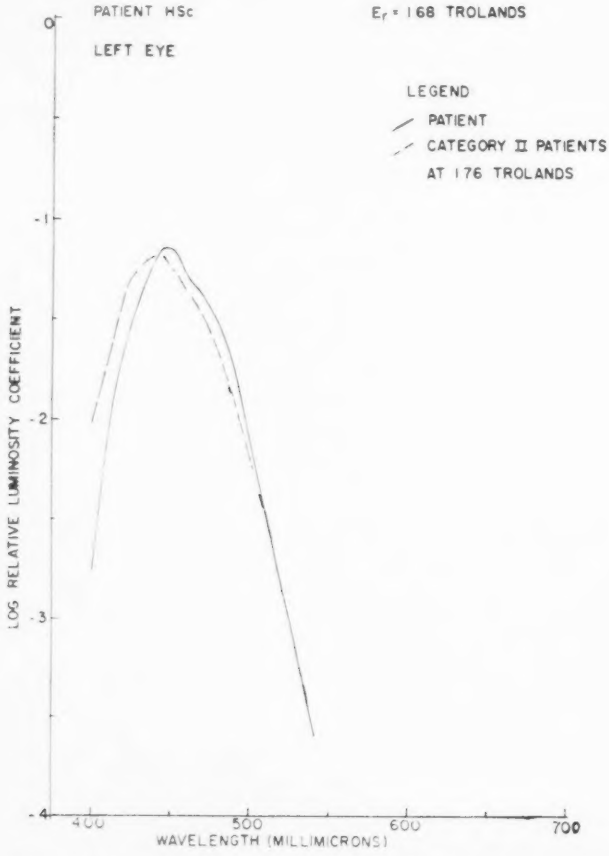

FIG. 25. Individual luminosity data for the left eye of patient HSc compared with analogous data for Category II patients. The Category II coefficients adjusted along the ordinate for best overall agreement with the data.

Peripheral dark-adaptation data (two tests) for white and blue test stimuli are presented in Fig. 27. Viewing was monocular. The ordinate scale refers to the white test data, the blue test data having been adjusted by a density value of 1·07. It is clear that rods mediate the entire course of peripheral dark-adaptation. It is also quite apparent that there are two segments in the dark-adaptation curve. The quantitative resemblance of these data to those of the Category II patients, presented in Fig. 12, is striking.

The luminosity and dark-adaptation data thus appear to have identified the patient unmistakably as a member of Category II.

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In attempting to measure the acuity function of illuminance, we first became aware of a marked difference between this patient and the Category II patients. The present patient reported that he could not take the letter acuity test without what he called "squinting". A long series of investigations finally established that the patient had voluntary control of gross nystagmus. Nystagmic movements were initiated under voluntary control at high levels of illuminance apparently because of numerous functional scotomata existing near the

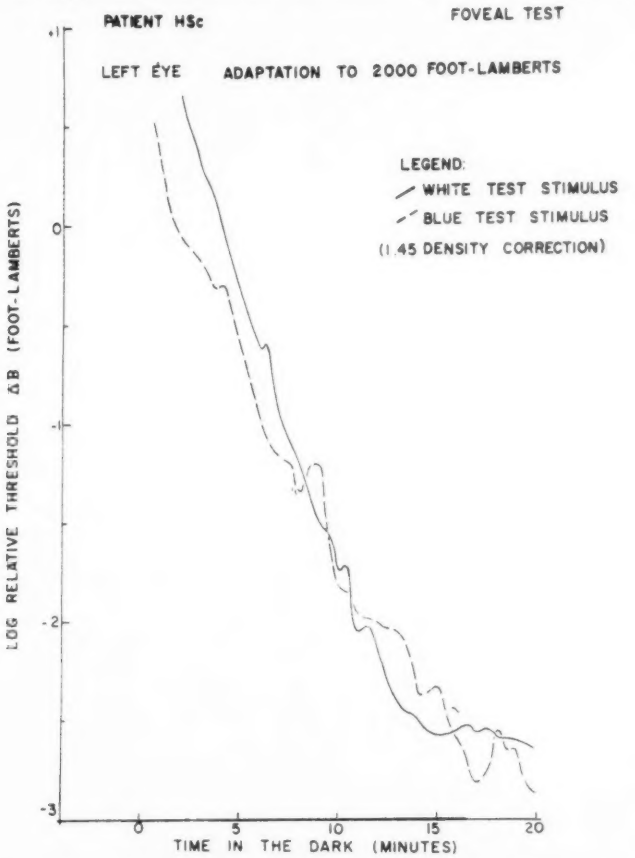

FIG. 26. Individual foveal dark-adaptation data for the left eye of patient HSc with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·45.

fixation point which obliterated portions of objects of regard. The patient induced nystagmus apparently to obtain continuity of the image even though image-sharpness was reduced.

The physical characteristics of the voluntary nystagmus were determined by electrical measurements of eye position, based upon the resting potential of the eye, or electro-oculograph as MARG (1951) has called it. Equipment and procedures developed earlier by LAW and DEVALOIS (1958) were used.[4] These measurements revealed that the mean amplitude of ocular movement under the "no squint" condition was $\pm 0{\cdot}6°$. When the command was given to "squint", the mean amplitude increased to $\pm 2{\cdot}5°$. There was also

[4] Measurements made by Professor Mathew Alpern of The University of Michigan.

sometimes a 2° lateral movement of the eye to the right, which moved the fixational center to an eccentric point 2° away from the fovea centralis into the nasal retina.

We made every possible effort to determine what retinal location was used in the "no squint" condition. Blind spot mapping and entrance pupil studies suggested that fixation in the left eye was at the fovea centralis. Use was made of the entoptic appearance of the macula, often called Maxwell's spot. Contrary to the expectation of WALLS and HEATH (1954), the patient was able to see and draw Maxwell's spot. For the unsquinted left eye, the spot was precisely centered on the point of fixation. Thus we may presumably conclude that the patient used foveal fixation ordinarily with this eye. Eccentric fixation in the amount of 2° was an incidental accompaniment of the production of nystagmus by squinting.

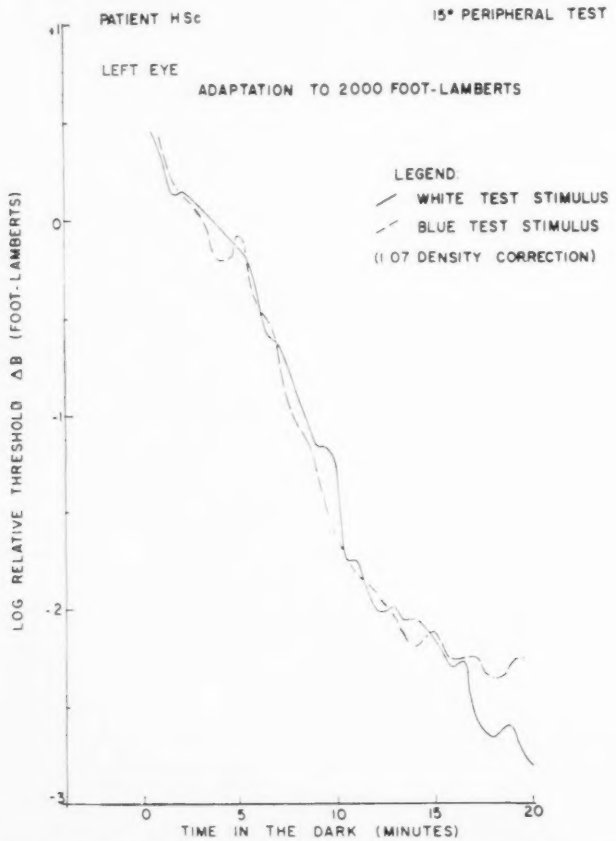

FIG. 27. Individual peripheral dark-adaptation data for the left eye of patient HSc with white and blue test stimuli. Blue test data adjusted along the ordinate for a density correction of 1·07.

The patient reported that he was able to induce nystagmus only at relatively high levels of illuminance. It was therefore believed not possible to measure luminosity with nystagmus at the lower level of illuminance. The luminosity data (eight sets) obtained by the patient with his left eye in nystagmus at high levels of illuminance are presented in Fig. 28, with comparable data obtained by the Category III patients. It is apparent that the agreement between the two sets of data presented in Fig. 28 is extraordinarily good. The patient

noticed hue-differences between various combinations of wavelengths. Accordingly, he was given single presentations of various wavelengths of the spectrum in a random order, equated for luminosity, and was asked to give color names to different parts of the spectrum. The patient used the color name "blue" for all wavelengths from 400 to 450 mμ, the name "gray" for wavelengths between 450 and 470 mμ, and the name "yellow" for all wavelengths longer than 470. Thus, he exhibited dichromatic color-discriminations based presumably on blue cones and rods. The Category III patients did not make color-

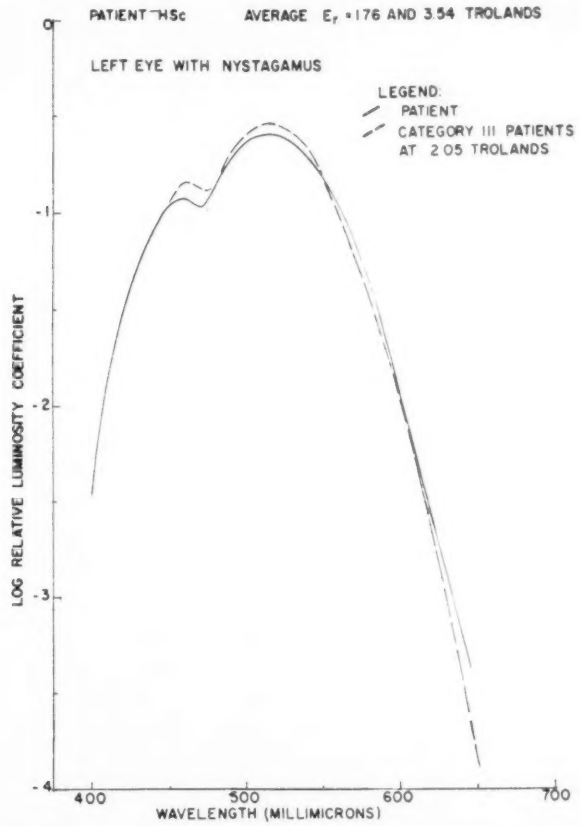

FIG. 28. Individual luminosity data for the left eye of patient HSc with voluntary nystagmus compared with analogous data for Category III patients. The Category III coefficients adjusted along the ordinate for best overall agreement with the data.

discriminations under these conditions. However, unlike the present patient, these patients had presumably never operated with a large number of blue cones, and hence may not have learned to make the color-discriminations of which they were theoretically capable.

The present patient was able to obtain white light acuity data at various illuminance levels, provided that he was allowed to "squint" when he felt it necessary. The data (six tests) he obtained are presented in Fig. 29, together with the acuity data for the Category III patients. It is apparent that the agreement between the two sets of data is excellent, particularly at the higher levels of illuminance. In this connexion, it is interesting to report that the patient was aware of "squinting" at all values of retinal illuminance greater than 100

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trolands, but believed he was not squinting at lower illuminance levels. It is at the acuity levels at which the patient was aware of squinting that the acuity data agree so well with the data from the Category III patients.

Acuity data (three tests) were also obtained for patient HSc with blue light. These data are compared with the patient's white light data in Fig. 30. As usual, the abscissa scale refers to the white light data, the blue light data having been adjusted by a density value of 1·60. The agreement between the two sets is excellent, revealing that the lower segment of the acuity curve is mediated by rods.

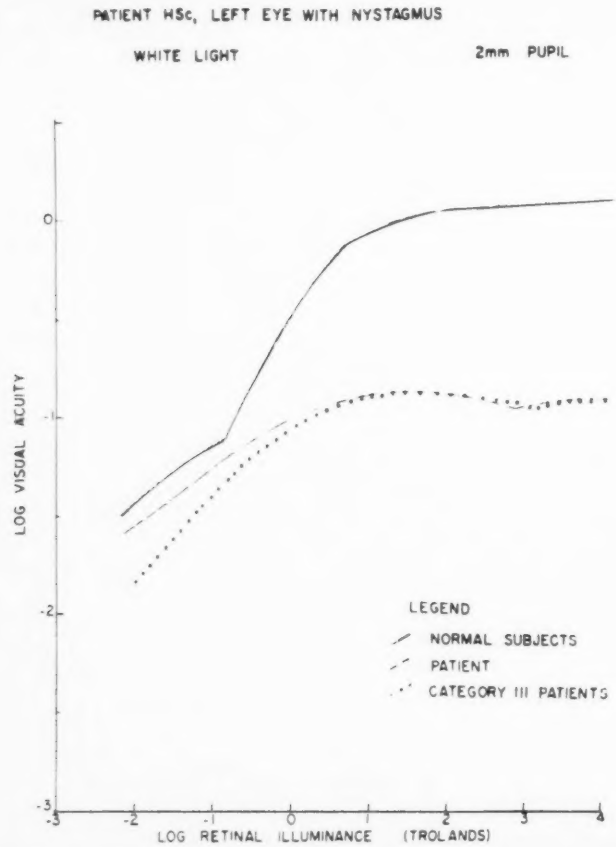

FIG. 29. Individual acuity function of illuminance for the left eye of patient HSc with voluntary nystagmus compared with analogous data for Category III patients, and for normal subjects.

The luminosity and acuity data thus seem to have unmistakably identified the patient when "squinting" and using his left eye as a member of Category III.

The patient was found to suffer from alternating suppression. He normally used the left eye and allowed the right eye to deviate by about 30°. However, the patient could bring the right eye into what appeared to be the straightahead position and did so whenever he was concerned about his appearance. He made it a habit to use his right eye and to allow his left eye to deviate from time to time to rest his left eye.

The patient was able to see Maxwell's spot in the right eye. The entoptic image was not centered about the point of fixation nor was the patient able to force his eye into foveal fixation when viewing a bright extended source during the plotting of the image. The position of the entoptic image revealed that the patient's right eye fixation fell at a point 4·5° into the temporal retina from the fovea centralis. Electrical measurements revealed that, under monocular conditions of observing, the right eye exhibited a mean amplitude of ocular movement of ±0·75°. The patient believed he was unable to "squint" with this eye.

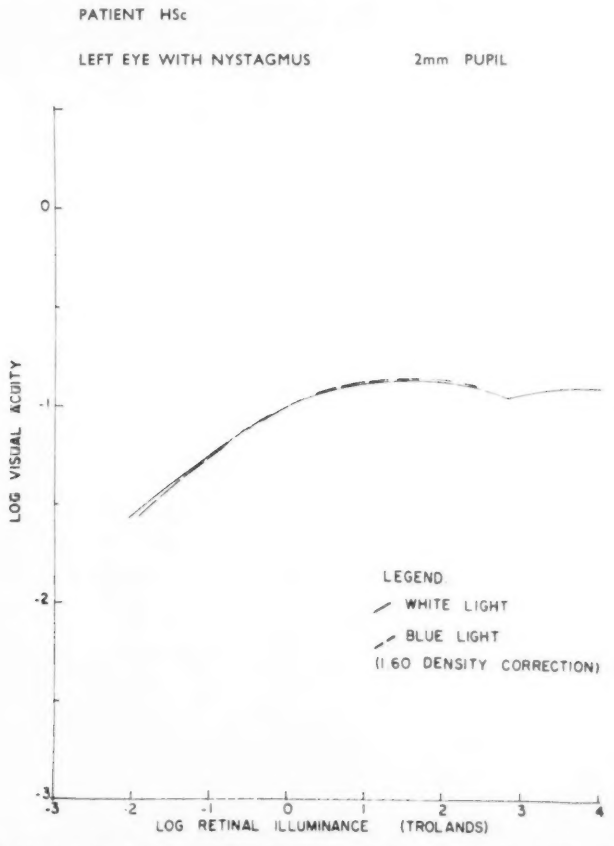

FIG. 30. Individual acuity function of illuminance for the left eye of patient HSc with voluntary nystagmus for white and blue light. Blue light data adjusted along the abscissa for a density correction of 1·60.

However, when commanded to "squint", the right eye sometimes moved 2° to the right and the mean amplitude of ocular movement increased to ±3°. When the eye moved in squinting, this reduced the eccentricity of fixation from 4·5 to 2·5° into the temporal retina.

Luminosity measurements were made by the patient using the right eye. Measurements were made at a range of illuminances from 0·0744 to 1·78 trolands. At none of the illuminance levels was the patient able to discriminate one wavelength from another consistently. Since the data were very similar at the various illuminance levels, averaged data (seven tests) are presented in Fig. 31, with the standard CIE Scotopic curve plotted for comparison. In

view of the excellent agreement between the data and the Scotopic curve, we may here consider the patient unmistakably classified as belonging to Category I.

Acuity data (three tests) as a function of luminance are presented for the patient's right eye in Fig. 32, obtained with white light. Acuity data for the Category I patients are presented for comparison, and the two sets of data are shown to be in excellent agreement.

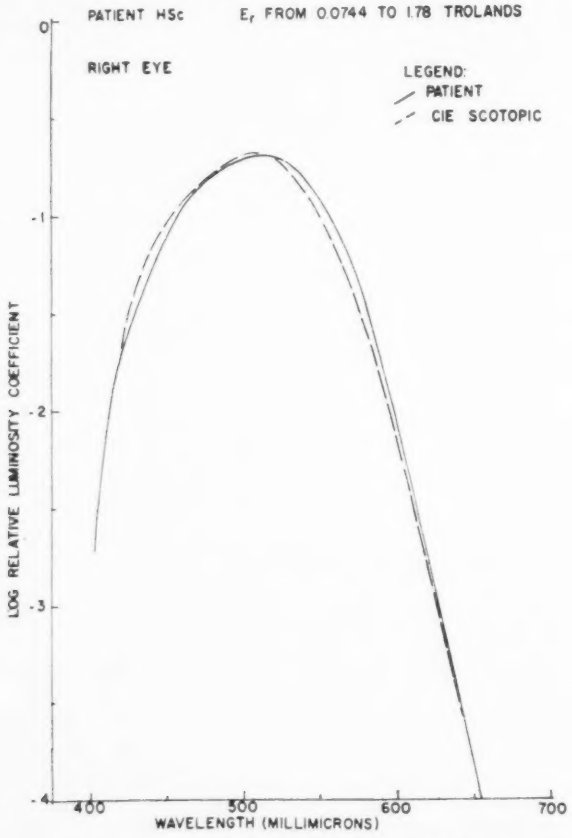

FIG. 31. Individual luminosity data for the right eye of patient HSc compared with standard scotopic luminosity coefficients. Scotopic coefficients adjusted along the ordinate for best overall agreement with the data.

The luminosity and acuity data thus appear to classify the patient's right eye unmistakably as belonging to Category I. However, as we have seen, the patient's left eye without nystagmus may be classified in Category II and the left eye with nystagmus may be classified in Category III. It thus appears that the three categories of congenital achromatopsia can all be found within this one patient, depending upon eye and/or mode of fixation used.

DISCUSSION

Repeatedly through the foregoing sections, we have adjusted foveal and peripheral dark-adaptation and acuity data obtained with white and blue light to establish the number and spectral sensitivity of the receptor systems responsible for the visual functions. The adjust-

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ment factors used to identify rods are summarized in Table 2 for the three visual functions.

TABLE 2. SUMMARY RESULTS FROM SPECTROPHYSIOLOGICAL ANALYSES: ROD RECEPTORS

A. Foveal dark-adaptation

Patients	Density adjustment factor
Category I	1·07
Category II	1·45
Category III	1·59
HSc	1·45
Average	1·39

B. Peripheral dark-adaptation

Patients	Density adjustment factor
Category I	1·33
Category II	1·45
Category III	1·71
HSc	1·07
Average	1·39

C. Acuity

Patients	Density adjustment factor
Category I	1·20
Category II	1·37
Category III	1·70
HSc	1·60
Average	1·47

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It is apparent that there is fairly large variation in the values but that the average values for the three tests are quite similar. It is to be recalled that the theoretical density computed on the basis of the CIE Scotopic curve was 1·45 for the dark-adaptation data and 1·37 for the acuity data. The average empirical factors for these tests do not differ from each other in the expected direction, but the variability among individual values is great enough so that this is not surprising. The important thing is that the average factors are in reasonable agreement with the average theoretical density values so that our identification of rod receptors from spectrophysiological analysis may be considered justified.

It should be reported that the density of the blue filter is computed to be 0·03 greater for rods modified by 10 per cent xanthophyll and 0·21 greater for rods modified by 70 per cent xanthophyll than for unmodified rods. It is to be expected that the factors obtained in foveal dark-adaptation and acuity will reflect these values for the patients exhibiting these quantities of xanthophyll in their luminosity data. The data in Table 2 are not sufficiently precise to warrant detailed analysis but it appears that the average factors agree better with the expected densities for normal rods than with the expected densities for xanthophyll-modified rods. This may signify that our patients used peripheral rods in both "foveal" dark-adaptation and in the acuity measurements at low luminance. Fortunately we have precise luminosity data to establish that rods did exist in some cases beneath a large concentration of xanthophyll, since we apparently cannot determine a matter of this small magnitude from our analysis of dark-adaptation or acuity data.

The fact that patient HSc resembled in detail each of the three categories of congenital achromatopsia when using a different eye and/or mode of fixation strongly suggests that the nine patients we have studied have the same type of receptors, blue cones and rods, and differ principally in the mode of fixation used. It was not possible for us to subject this

hypothesis to rigorous test, principally because by the time analysis of our data was completed, the original patients were no longer available for study. Of course, our medical findings confirm the notion that Category III ordinarily corresponds to gross nystagmus, since only patients FB and HP exhibited this abnormality. Ordinary clinical methods are not sufficiently sensitive to pick up with certainty an eccentric fixation of the order of 4·5°, although special techniques such as that recently proposed by VON NOORDEN *et al.* (1959) would seem able to do so. One difficulty which became apparent to us in further study of

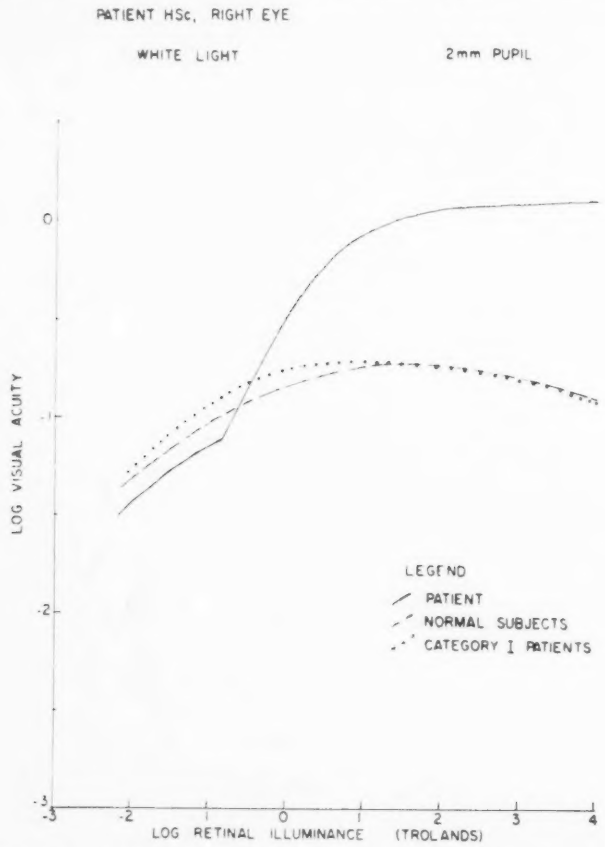

FIG. 32. Individual acuity function of illuminance for the right eye of patient HSc compared with analogous data for Category I patients, and for normal subjects.

patient HSc is that the mode of fixation can change without the patient's awareness both with respect to the eccentricity of fixation and the degree of nystagmus. This implies that assessment of fixation by available techniques such as Von Noorden's is not entirely satisfactory. What is needed is a method of determining the retinal locus of fixation at all times during psychophysical measurements, without alteration of the psychophysical function. None of the existing ingenious optical or electronic methods of measuring eye-movements can satisfy this requirement. The entoptic macular image is a very useful technique although most patients do not experience the phenomenon readily. So long as these limitations exist, perhaps our quantitative evaluation of fixation modes in patient HSc, together with the

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demonstrated equivalence of his psychophysical data to those of the various categories of congenital achromatopsia, constitute the best evidence for our hypotheses.

There are a few loose ends in our account which can be tied together now that our report of data is complete. Using the fixation data from patient HSc to represent each of the three categories of achromatopsia, we may draw the following tentative conclusions. Category I normally corresponds to eccentric fixation of about 5°, without nystagmus. Category II corresponds to foveal fixation without nystagmus. Category III normally corresponds to gross nystagmus, more or less centered about the fovea.

The psychophysical data we have obtained may be used to identify the probable locus of the blue cone and rod receptors. Both types of receptors appear to be located in the fovea centralis. With eccentric fixation of 5°, there is no evidence of blue cone activity. We may reasonably suppose that the number of blue cones is greatest at the fovea and becomes progressively smaller at increasingly more eccentric locations. The patients with nystagmus are smearing the retinal images of our test objects across the retina, averaging some of the blue cones located within or near the fovea with the larger number of rods located at the fovea and elsewhere. Presumably it would be possible to arrive at the same proportion of blue cones and rods either by nystagmic averaging or by selecting an eccentric locus of fixation less than 4·5° from the fovea centralis. Although the blue cone–rod ratio might be the same, the presence of smearing due to nystagmus would presumably differentiate between the two hypothetical classes of patients.

The number of blue cones within the fovea varies among different patients. If this were not so, patient HSc presumably could have obtained an acuity function similar to that obtained by the Category II patients. When the number of blue cones is comparatively great, the patients will have a maximal acuity of about twenty in sixty and will not have to use nystagmus to preserve continuity. When the number is comparatively small, the patients will either have to use nystagmus or eccentric fixation in order to preserve continuity.

The acuity data for the three categories of patients, exhibited in Fig. 21, may be used to further develop these notions. At low luminances where only rods are involved in the acuity function, the Category I and II patients have higher acuity than the Category III patients. Since only the Category III patients have nystagmus, this may be taken as evidence that nystagmus reduces the maximum acuity of which the rods are capable. It is also to be noted that the maximum acuity of the rods is greater for the Category I than for the Category II patients. This could be explained on the basis that the rods are more closely packed at the eccentric location used by the Category I patients than they are at the fovea, due to the spaces occupied by blue cones.

It has not been made clear why some patients use eccentric fixation while others use nystagmus. It has been suggested by WALLS and HEATH (1954) that congenital achromats usually have gross nystagmus early in life but outgrow it. Our data on the members of the St family could be used to support this hypothesis. Our patient HSt did not show gross nystagmus at age twenty-two whereas his younger brothers DSt and JSt showed gross nystagmus at ages twelve and nine respectively. It is not known whether or not HSt had gross nystagmus when he was younger. None of the members of the B family had gross nystagmus when examined, not even RB who was only six. It could be postulated that nystagmus results whenever there are enough blue cones in the fovea to give this retinal area an advantage over the periphery with regard to acuity at high luminance. Eccentric fixation results whenever the foveal blue cones are simply too scarce to provide a useful function even at high luminance. The gradual loss of nystagmus could mean the gradual loss of blue

cones. In these cases, we would have to consider congenital achromatopsia as a progressive heredo-degenerative retinal disease, which is certainly an unconventional view.

Thus far we have not demonstrated directly that there are blue cones in a Category I eye. We have tacitly assumed that there are blue cones in the right eye of patient HSc because blue cones have been shown to exist in his left eye. One final set of luminosity data obtained on the right eye of patient HSc may be used to establish that there are, indeed, blue cones in

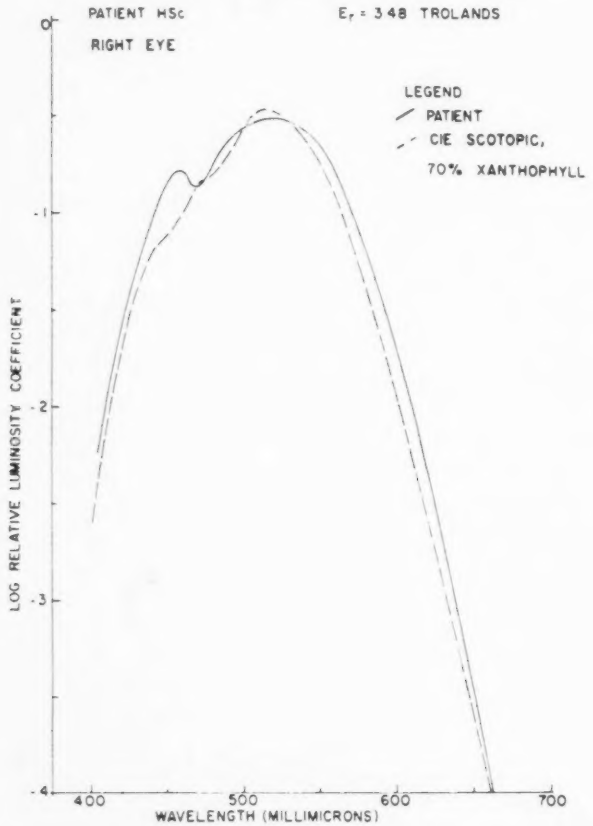

FIG. 33. Individual luminosity data for the right eye of patient HSc compared with standard scotopic luminosity coefficients modified by absorption of a 70 per cent concentration of macular xanthophyll. Scotopic coefficients adjusted along the ordinate for best overall agreement with the data.

a Category I eye. A 402 mμ standard was used at 3·48 trolands, a higher level than had been used in collecting the data reported heretofore. The data are presented in Fig. 33, together with the CIE Scotopic curve modified by a 70 per cent concentration of xanthophyll. The luminosity data for wavelengths longer than 475 mμ are reasonably well fitted by this curve and cannot be fitted by the standard CIE curve. The luminosity data at wavelengths less than 475 mμ show evidence of the existence of blue cones. These data bear a striking resemblance to the data obtained by the patient with the left eye under voluntary nystagmus, which are presented in Fig. 28. The patient was able to make color-discriminations between

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the standard and wavelengths in the range from 520 to 600 mμ. He called the 402 mμ standard "blue" and the comparison wavelength "yellow".

These data are most interesting because they establish that a Category I eye can be shown to contain blue cones, under rather extreme circumstances. The fact that the data fit the Scotopic curve with a 70 per cent concentration of xanthophyll establishes that the patient must have been utilizing rods situated beneath the concentrated layer of this pigment which is located at the fovea. Thus, by using an intense blue standard, we induced the patient to overcome his usual suppression of the foveal area of the right eye. These results suggest that the study of the functional characteristics of the receptor systems existing in strabismus may suggest conditions for training which may prove useful to the patient.

Since our major conclusion is that all congenital achromats with low acuity have both rods and blue cones, it may seem that we are in agreement with the hypothesis of WALLS and HEATH (1954) to this effect. Although our conclusion is the same, we do not share Wall's and Heath's assumptions and regard their conclusion as incompatible with the data from which it was derived. Walls and Heath believed in the existence of blue cones, as well as rods, in the retinae of all congenital achromats in spite of the fact that all the psychophysical evidence available to them seems to contradict this conclusion. The luminosity data then available, like our data for the Category I patients, agreed with the standard CIE Scotopic curve. Walls and Heath explained these results by asserting that the blue cones did not contribute to luminosity. Walls and Heath supported their contention that blue cones existed in these eyes with the fact that peripheral dark-adaptation curves then available, like our data for the Category I patients, had a duplex form. We now know from the present work and the report of SLOAN (1957) that both sections of the dark-adaptation curves have the spectral sensitivity of rods.

Walls and Heath had available the HECHT (1948) data which demonstrated that the acuity function of luminance was apparently simplex in form. They explained this result by assuming that the acuity potential of rods and blue cones was the same. The acuity data of BRINDLEY (1953) utilizing chromatic adaptation of the red and green mechanisms seem to confirm this assumption since the acuity of blue cones was inferred to be about twenty in two hundred. On the contrary, our data on the Category II patients (Fig. 13) suggest that the acuity potentials of blue cones and rods are quite different.

Finally, Walls and Heath believed that the existence of blue cones and rods could not provide a basis for dichromatic color response, since in their view only cones can mediate color, and therefore blue cones must produce monochromatic color vision. On the contrary, we have shown that the existence of comparatively numerous blue cones and rods of nearly equal sensitivity provide the basis for a dichromatic color system.

SUMMARY

We have studied thirteen male cases of congenital achromatopsia with reduced acuity, including what have been previously designated typical and atypical cases. Twelve have been classified into three categories on the basis of precise psychophysical tests. The tests included measurements of luminosity, foveal and peripheral dark-adaptation; and the acuity function of luminance. In the acuity and adaptation tests, measurements were made with white and blue light to establish the spectral sensitivity of the receptors involved. Normal color vision tests including the Farnsworth–Munsell 100-Hue Test, and measurements on a Nagel-type Anomaloscope were not useful in classifying the patients. The following categories were identified:

Category I (Rod monochromacy). These patients have only functional rods and have no color-discrimination under any condition. There is no nystagmus.

Category II (Blue monocone monochromacy). These patients have blue sensitive cones, with a maximum sensitivity at about 440 mμ, and foveal rods, in which the normal rod luminosity curve is modified by the absorption of macular xanthophyll pigment in high concentration. At low luminance levels, the patients operate as rod monochromats. At high luminances, they operate as blue cone monochromats. At intermediate luminances, they operate as blue cone–rod dichromats. Both rods and blue cones appear in acuity and foveal dark-adaptation measurements, whereas only rods are involved in peripheral dark-adaptation. Rods and blue cones summate in luminosity but show mutual inhibition in acuity. There is no nystagmus.

Category III (Intermediates). These patients have rods and a few blue cones which are revealed in luminosity measurements at high luminance. The rods and blue cones appear in both acuity and foveal dark-adaptation but not in peripheral dark-adaptation. Vision is monochromatic under all conditions. Some siblings of Category I patients fall into this category.

The thirteenth patient was identified with each category, depending upon the eye and/or mode of fixation used. When foveal fixation was used without nystagmus he resembled the Category II patients. When foveal fixation with voluntarily induced nystagmus was used, he resembled the Category III patients. When eccentric fixation was used without nystagmus, with a normally suppressed eye, he resembled the Category I patients. With a strong stimulus in blue light, the patient was encouraged to use foveal fixation with the normally suppressed eye, and evidences of blue cones were found.

We conclude that probably all cases of congenital achromatopsia with reduced acuity have both rod and blue cone receptors, the latter varying in number among different patients. With a normal number of blue cones, the patients use foveal vision and fit Category II. With fewer blue cones, they exhibit nystagmus in order to gain the benefit of the blue cones at high luminance levels, and fit Category III. With still fewer blue cones, they use eccentric fixation and fit Category I. The fact that nystagmus often disappears in congenital achromatopsia with maturation may mean that the blue cones become functionally inoperative with age. This would imply that congenital achromatopsia is an heredo-degenerative disease of the retina.

The theoretical significance of the discovery of blue cones in isolation will be treated more fully in a forthcoming paper.

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A STUDY OF BINOCULAR COLOR MIXTURE

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Abstract—Using an apparatus which presents simultaneously the components for binocular color mixing to each eye and an additive, comparison mixture of the components to both eyes, an investigation was made of the effects of stimulus size, exposure time, and surround on the frequency with which the observers reported matching binocular mixtures. A comparison of binocular with additive mixtures as a function of (1) their relative total luminances using equal binocular components and (2) variable binocular composition with constant total luminance was also carried out. A brief history of work on binocular color mixture has been included.

Résumé—Avec un appareil qui présente simultanément les constituants d'un mélange binoculaire de couleur dans chaque oeil ainsi qu'un mélange additif de comparaison vu par les deux yeux, on a recherché les effets de la dimension, de la durée, et de l'environnement du stimulus sur la fréquence avec laquelle les mélanges binoculaires sont perçus. On a aussi examiné la comparaison des mélanges binoculaires avec les mélanges additifs en fonction (1) de leurs luminances relatives totales pour des constituants binoculaires égaux et (2) de constituants binoculaires variables pour une luminance totale constante. On a inclus un bref historique du problème du mélange binoculaire de couleur.

Zusammenfassung—Ein Apparat, der gleichzeitig jedem Auge je eine Farbkomponente für binokulares Farbensehen und zum Vergleich eine additive Farbmischung aus beiden Komponenten anbietet, wurde dazu benutzt, um den Einfluss der Reizgrösse, der Darbietungszeit und des Umfeldes von der Häufigkeit der beobachteten binokularen Farbmischungen festzustellen. Ein Vergleich von binokularer und additiver Mischung wurde bei gleichen binokularen Komponenten und bei gleicher totaler Leuchtdichte als eine Funktion (1) der relativen totalen Leuchtdichte und (2) der variablen binokularen Komponenten ausgeführt. Vorangegangene Arbeiten über binokulare Farbmischungen werden einleitend kurz erwähnt.

THE binocular mixture of colors was first reported by Haldat in 1806, and the succeeding early literature on the subject was largely concerned with the authenticity of the phenomenon. While many investigators vouched for it, a few were able to achieve only such related effects as oscillation or the dominance of one of the components (SOUTHALL, 1924).

This early literature was summarized by Helmholtz and Hering, who, as was often the case, took opposite points of view on the question. From his unsuccessful attempts, Helmholtz (SOUTHALL, 1924) concluded that the alleged binocular mixtures were due to background induction, the absence of a uniocular comparison field, or the presence of afterimages. HERING (1864) believed that binocular mixture was always possible if certain precautions were taken: the colored areas should be small and the same in shape, contour differences should be minimized, the colors should be of equal brightness and not widely separate in hue; complementary colors could be mixed if they were unsaturated and dull.

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The demonstration devised by HECHT (1928) has become the standard method of binocular mixture. He placed a red (Wratten No. 29) and a green (No. 58) filter side by side at one end of a black box; at the other end was a white piece of cardboard. On looking at the cardboard through the filters, he saw a yellow square flanked by a green and a red square.

MURRAY (1939) argued that Hecht's results were vitiated by the particular red and green used. She rejected his conclusions on the grounds that (1) the filters were wide band yellow–green and yellow–red, (2) the intensity used was too high for this type of color filter, (3) the procedure favored the focusing power of the lens for yellow radiation and the fusion area fell within the *macula lutea*, the yellow-enhancing region of the retina and (4) no time limit was set for the observations, possibly allowing adaptation to cancel the red and green.

In reply to Murray's criticisms, PRENTICE (1948) repeated Hecht's procedure using sharp cut-off interference filters, three light levels and a short exposure time. He found that even when exposed for 2 sec at his lowest stimulus brightness, red and green combined binocularly to give a yellow comparable to a spot of light projected on the screen through a yellow interference filter. A long exposure time (30 sec or more) gave a better yellow.

Very few studies have investigated the extent to which the binocular mixture resembles the same mixture to a single eye. The first quantitative study was by TRENDELENBURG (1923). To achieve binocular mixture, he found it necessary to use a very small stimulus, often less than 30 min of arc, but he succeeded in combining spectral red and green to get a white resultant which was compared, from memory, to the monocular mixture. In this and a later study (1923), he found that a much smaller proportion of the shorter wavelength was required in the binocular stimulus.

ROCHAT (1922), on the other hand, found that in binocular mixtures a little less of the longer wavelength was required. He projected complementary colors to a surface on which there was a white comparison field. By appropriately converging his eyes, he was able to compare the binocular mixture with the comparison field as well as with a monocular mixture of the combined complements. Both blue and yellow as well as red and blue–green gave a match to white. He could not, however, obtain a binocular match within the region from 610 to 570 mμ.

LIVSHITZ (1940), with an optical system consisting of a spectroscope and a double monochromator, was able to present a comparison field of combined monochromatic colors to each eye while the color components for the binocular combination were presented to an adjacent area of each retina. The intensities of the monochromatic fields were photometrically balanced and the spectral region from 640 to 530 mμ was matched monocularly and binocularly at 10 mμ intervals by combining 670 and 517 mμ. From 640 to 580 there was close agreement between all the matches. From 570 to 540 much less red was needed in the binocular match. Thus, in the region where Trendelenburg found a difference between monocular and binocular red–green mixtures, Livshitz found close agreement. But the differences in the spectral green used and the mode of presentation of the comparison field may account for this.

The present study has investigated the effect of various experimental conditions on the binocular mixture of colors and has compared binocular mixtures to adjacent additive mixtures presented simultaneously.

APPARATUS

The color mixer used in this study presented simultaneously to each eye a circular bipartite field. In the upper half of each field appeared an additive mixture of two color

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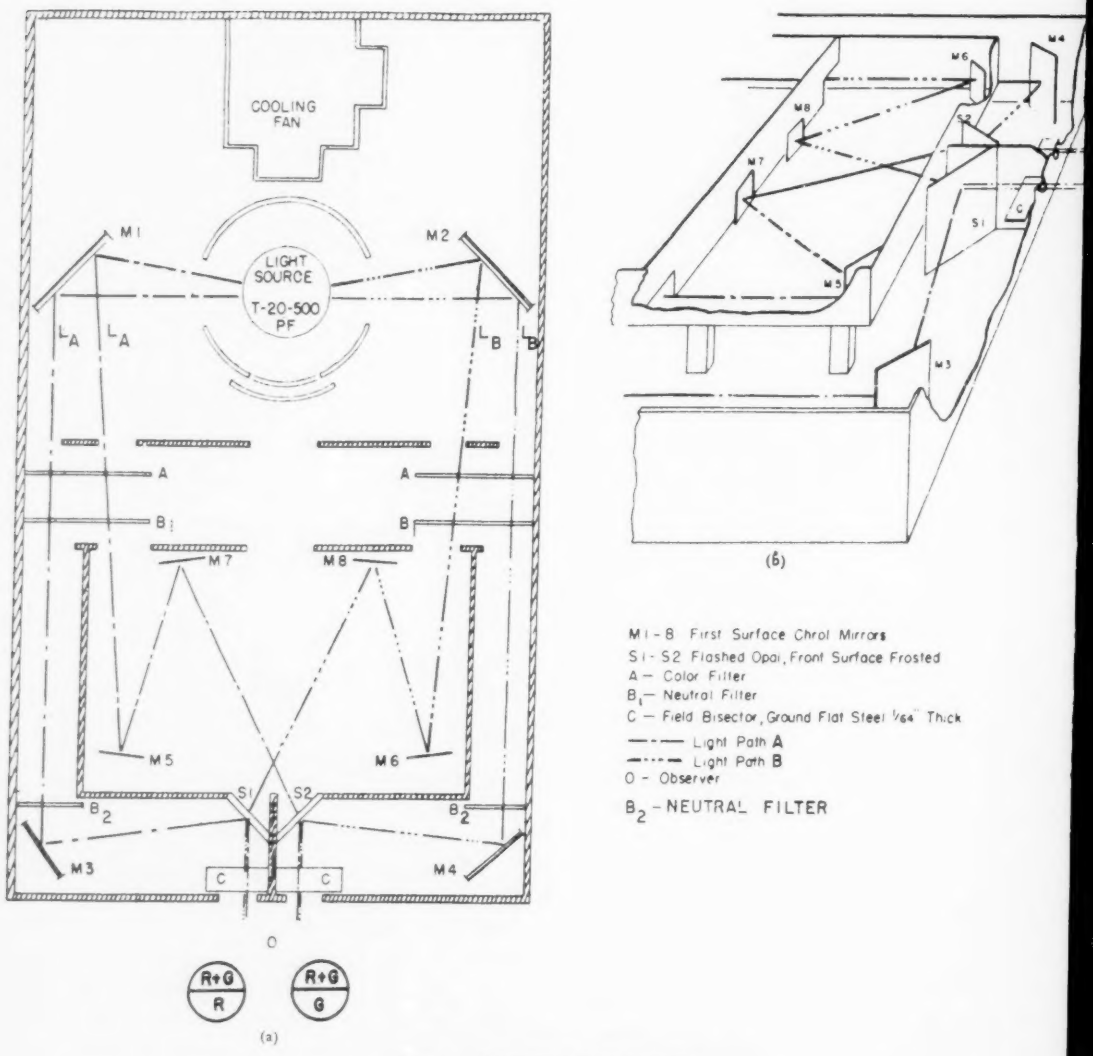

FIG. 1. Diagram of the apparatus.

components, which served as a standard or comparison mixture. In the lower half, one of the color components was presented to each eye for binocular mixture. The schematic drawings of the apparatus in Fig. 1(b) show how this was done. Light from a 500 W lamp of color temperature 3142°K was reflected by chroluminum mirrors, M_1 and M_2, through colored and neutral filters at A and B, after which it was split into two beams by pairs of mirrors at M_3 and M_5, or M_4 and M_6. One beam of each pair (i.e. from M_3 and M_4) was reflected to the whole area of the white diffusing screen (ground opal glass) at S_1 or S_2. The other beam (i.e. from M_5 or M_6) was reflected from mirrors M_7 or M_8, through the upper half of the opal glass screens at S_1 or S_2, to mix with the light from M_3 or M_4 falling on the front surface of the screen (see insert, Fig. 1). Thus a given color component of the stimulus mixture was reflected from the entire front surface of one diffusing screen and was trans-

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mitted through the upper half of the other opal glass screen. One color was transmitted to the right eye and reflected to the left eye while the second color was reflected to the right eye and transmitted to the left eye. The mirrors and the glass opal screens were non-selective in the visible region of the spectrum.

Size of the stimulus was controlled by circular apertures set in front of the color mixing screens. The distance between the apertures was 2 in. center to center. The observer viewed the apertures from a distance of 18 in. through prisms held in a head-rest, which were adjusted to give precise registration of the binocular fields.

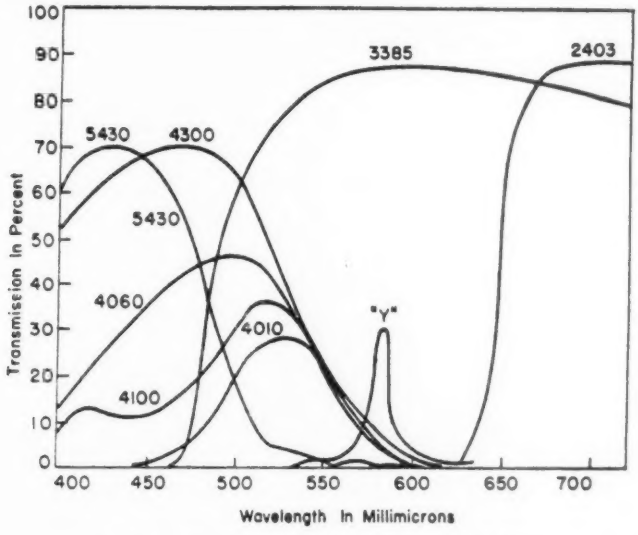

FIG. 2. Spectral transmission curves of the filters.

For a light surround, the white cardboard front of the apparatus was illuminated uniformly over an area subtending 20° visual angle by a Macbeth lamp (Illuminant C). The stimulus fields were occluded by a manually operated shutter on whose front were two luminous dots which served to orient and converge the eyes prior to stimulus presentation when a dark surround was used.

The maximum luminance of the beam reflected from the opal glass screen was 68 ft–L; that of the transmitted beam was 24 ft–L. The binocular mixture field and stimulus mixture field were equated for luminance by inserting neutral density filters in the appropriate light paths (i.e. at B_2).

The colors were produced by various Corning filters whose transmission curves are shown in Fig. 2. Their trichromatic specifications, dominant wavelength (λ) and purity (P) calculated for the light source of 3142°K color temperature, are given in Table 1.

PROCEDURE

The observer was seated with the head positioned by a head-rest. The bipartite stimulus fields were brought into register using the horizontal bisecting line as the alignment indicator. The observer was adapted to the surround brightness for five minutes, and given the following instructions: "At the signal 'now' a disk bisected by a horizontal line will be exposed. You are to judge whether the lower half of the disk is the same color as, or a different color

TABLE 1. SPECIFICATIONS OF THE COLOR FILTERS

Corning filter No.	x	y	Y	(λ)	P (%)
2403	0·728	0·272	0·029	655	1·00
3385	0·495	0·473	0·825	580	0·93
4010	0·248	0·633	0·116	539	0·72
4100	0·206	0·514	0·133	516	0·39
4060	0·195	0·403	0·159	500	0·38
4300	0·169	0·312	0·172	491	0·53
5430	0·150	0·103	0·032	471	0·84
Baird yellow "Y"	0·493	0·505	0·102	577	1·00

from, the upper half. If the lower half of the disk is a different color, report in what direction it differs."

Two seconds before the stimulus exposure, a ready signal was given. Rest periods were given after about thirty presentations.

1. PRELIMINARY EXPERIMENTS

An attempt was first made to ascertain the effect of the experimental conditions on binocular color mixture. Three stimulus variables were manipulated to determine their influence on the frequency with which such mixtures were reported, namely, stimulus size, exposure time, and surround brightness. The apparatus did not provide wide enough variations of stimulus intensity for complete investigation of this variable.

When a 5° stimulus field was used, the observers agreed that this area presented a mottled appearance which led them to confine their judgments to the center of the field. On this basis, a 2·5° stimulus was used in succeeding work and size appears as a variable only in the data of the preliminary experiment.

Five staff members (A. Morris, C. Pratt, J. Smith, E. Sandberg and R. Derby) with observing experience participated as observers in the preliminary work. All had normal color vision and wore spectacles for 20/20 vision when necessary. They were presented with stimuli produced with Corning glass filters of dominant wavelength 655 mμ (see Table 1) and 471 mμ paired with each other and each of them was paired with 539, 500, 516, and 491 mμ; 471 mμ was also paired with 580 mμ. The test pairs of stimuli were presented at five luminance levels in 0·1 density steps on the wedges; the test field was equal in luminance to the comparison field at the 0·3 density setting. They were first exposed for 2 sec in a 5° field with a surround which was either black or 10 per cent brighter than the stimulus. Next, 2·5° stimuli were presented under the two surround conditions for 6 sec. Each pair was presented at least thirty times in random order. A total of 3324 combinations was presented, 1662 under each surround condition, 1584 with the 2 sec exposure and 1740 with the 6 sec exposure.

The percentages of binocular color-mixtures matching the comparison field under the various conditions are given in Table 2. Increasing the exposure time from 2 to 6 sec produced five times as many binocular matches, while introducing a light surround reduced the number of matches by half for the 6 sec exposure time.

The composition of the binocular mixtures were averaged for all stimulus series in which six or more reports of "same" were given, and the percentage by which a binocular com-

ponent differed from the corresponding comparison component was computed. Some deviation of the binocular components from the comparison components was the rule. The average difference was less than 10 per cent, although the extreme difference was 53 per cent. The brightness of the surround showed no systematic effect on the composition of the binocular mixture.

TABLE 2. THE PER CENT OF PRESENTATIONS RESULTING IN BINOCULAR MATCHES UNDER VARIOUS EXPERIMENTAL CONDITIONS

Surround	Exposure Time		No. Presentations
	2 sec (5° field)	6 sec (2·5° field)	
Dark	3·4	31·0	1662
Light	5·1	13·5	1662
No. of presentations	1584	1740	3324

It is noteworthy that the mixtures containing a red component generally show that an excess of red is required in the binocular mixture, but the binocular mixtures with a blue component required an excess of blue. There was only one instance of a mixture with both red and blue and here an excess of red was required. These results are plotted in Fig. 3 and show how the mixtures with 655 mμ as one of the components deviate toward the red region of the diagram. It will be noted that matches were obtained in the region between 585 and 610 mμ where Rochat was unable to do so.

The observers reported that frequently the binocular field was not stable, but fluctuated. Unless a color mixture was observed immediately, there was either oscillation between the components or one of them dominated. The oscillation decreased with time, however, and it appeared likely that a longer exposure time would further increase the number of binocular mixtures.

It was difficult to account for the effects of surround illumination. Why should a dark surround produce an increase in the number of matches? The explanation may lie in the fact that the light surround could not be evenly illuminated beyond a 20° visual angle. This unevenness was minimized, however, in the succeeding work with a diffusing medium in front of the lamp and a light surround was used since it permitted a much shorter period of preadaptation.

2. VARIABLE TOTAL LUMINANCE AND EQUAL BINOCULAR COMPONENTS

Two observers were presented with 2·5° stimuli exposed for 15 sec. The filter with a dominant wavelength of 655 mμ was paired with 539 mμ and 471 mμ was paired with 577 mμ. The former pair was presented at five levels and the latter at six levels of total luminance, with the two components always equal to each other. Both pairs were presented at least ten times (ES received 20 presentations of the first pair) in random order for a total of 270 presentations. The luminance of the comparison mixture was 1·5 ft–L and that of the surround was 5 ft–L. The observers were instructed to make no judgment unless the binocular stimuli were fused for several seconds, long enough to make an accurate comparison between the two fields.

The responses were classified as (1) unqualified judgments of "same", (2) same but lighter, (3) same but darker, (4) oscillating and (5) one component dominates. These tabulations are shown in Table 3. In each series of combinations for both observers, the combination most closely resembling the comparison mixture was most frequently judged unqualifiedly the same. That is, the binocular mixture matched the comparison mixture when the total binocular luminance equalled the luminance of the comparison mixture to

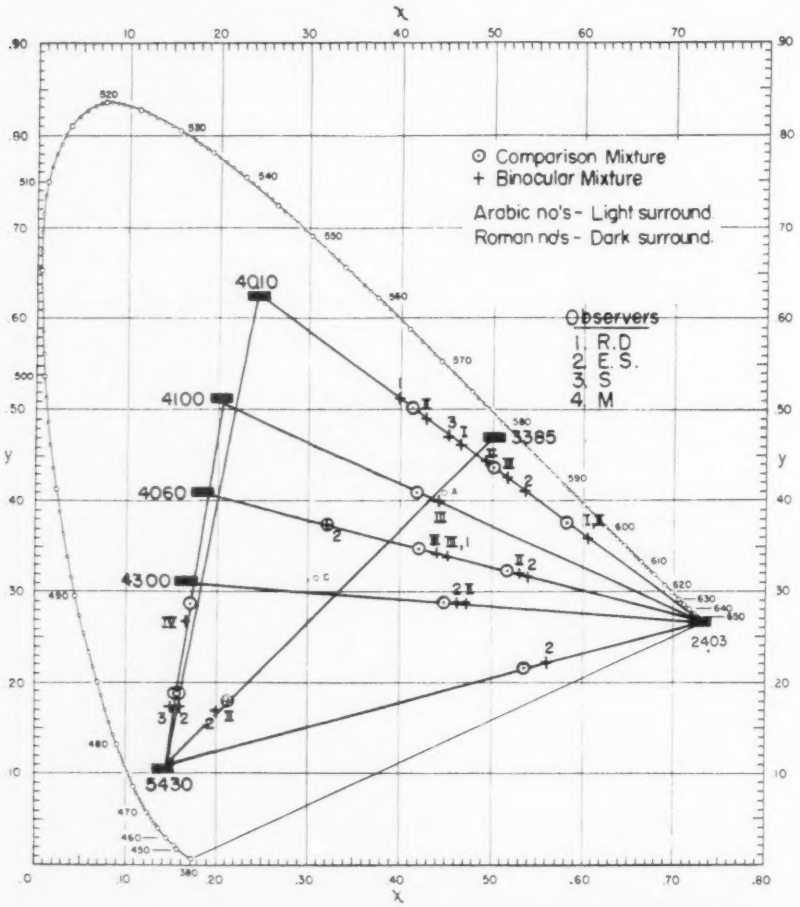

FIG. 3. Comparison of binocular and additive mixtures. The average chromaticities of the binocular mixtures for every series in which six or more reports of "same" were given compared to the chromaticities of the additive mixtures. Binocular mixtures with a red component usually required an excess of red.

only one eye. Since the comparison mixture, however, was presented to both eyes, this means that there was no summation of the two monocular fields. The luminance for two identical stimuli (one to each eye), then, is apparently not additive, while the luminances of two different stimuli, mixed binocularly, are additive.

Both observers more frequently judged the binocular mixture to be darker as it decreased in total luminance, but there were few reports of any mixture at all when the binocular

stimulus was brighter than the standard stimulus. Instead, this resulted in increasing oscillation. A darker binocular field, on the other hand, led to reports of dominance of one of the components.

Under these conditions, then, 33 per cent of the first pair of stimuli and 30 per cent of the second pair were judged unqualifiedly the same as the comparison mixture. An additional 19 per cent of the first pair and 35 per cent of the second pair were judged the same with qualifications. Thus, over half of the presentations resulted in binocular mixtures.

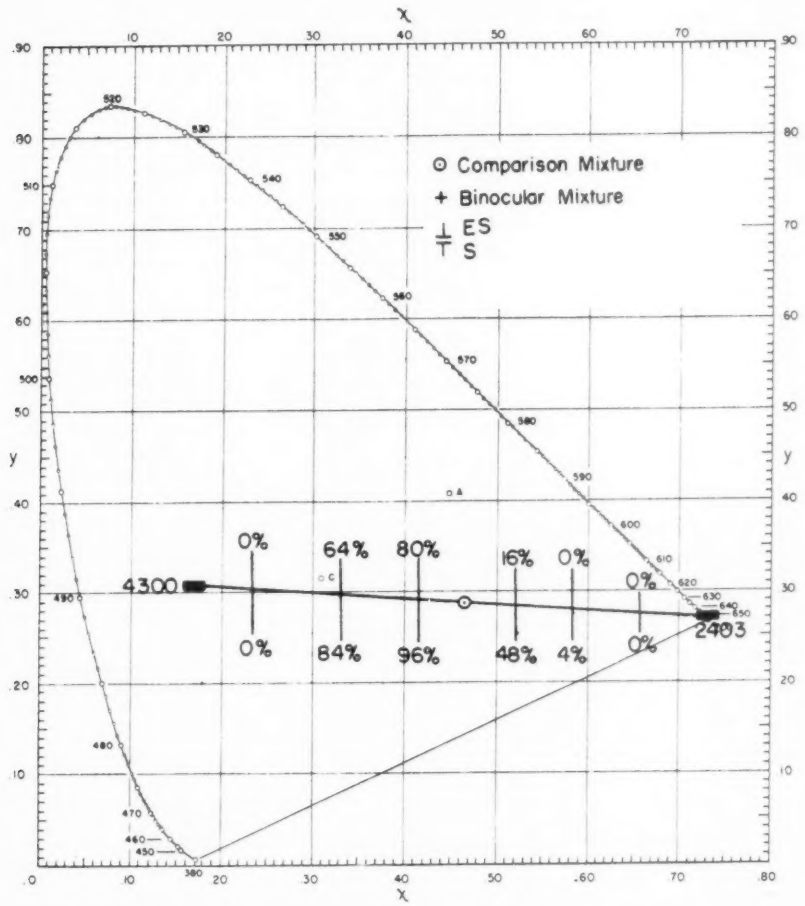

FIG. 4. The distribution of binocular match judgments. The per cent of "same" judgments for binocular mixtures of various compositions. The total luminance was constant.

The average value of the binocular components was computed for all unqualified judgments of "same" in each stimulus series. There was good agreement with the composition of the comparison mixture; the largest deviation was only 11 per cent. Thus with the exposure time increased from 6 to 15 sec and with a more even surround, the frequency of "same" responses increased and the disparity between the compositions of the comparison mixture and the average composition of the binocular mixtures judged the same decreased.

3. CONSTANT TOTAL LUMINANCE AND VARIABLE BINOCULAR COMPOSITION

Using the same procedure as outlined above, two observers were presented with the pairs 655–491 mμ and 471–577 mμ. The components in the comparison field were always equal to each other; but for the binocular field, six combinations of each pair were presented with varying proportions of the two components, with their total luminance constant. The luminance of the binocular components for the first pair ranged from 0·21 to 1·66 relative

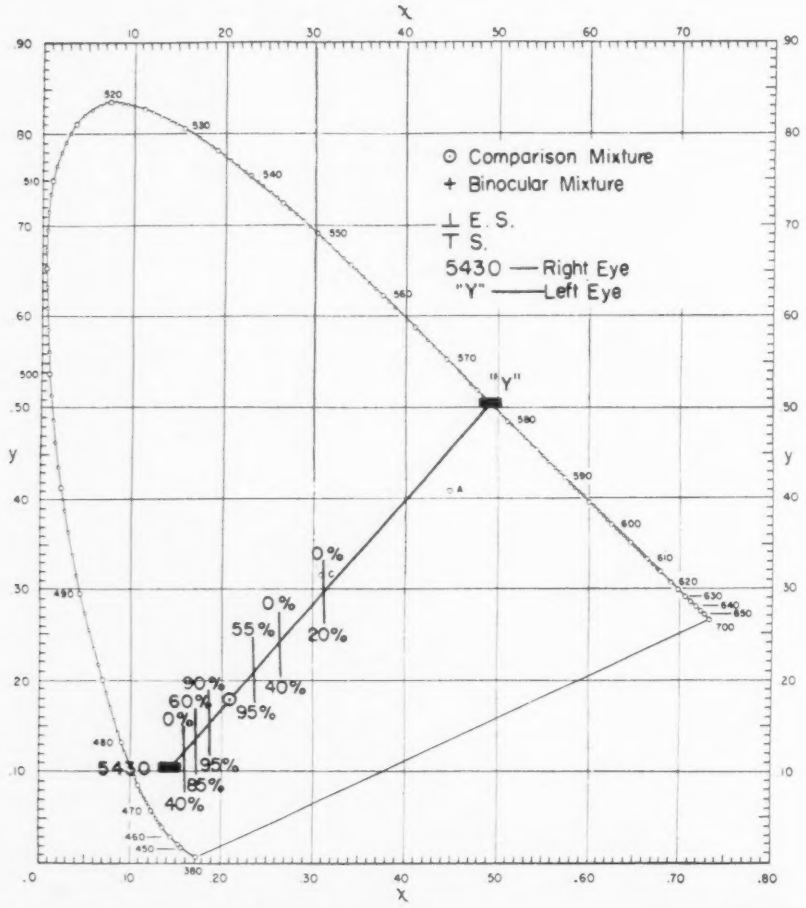

FIG. 5. The distribution of binocular match judgments. The per cent of "same" judgments for the binocular mixtures of various compositions. The total luminance was constant. Compare these values with those in Fig. 6 for which the binocular components were interchanged.

to the corresponding component in the comparison field and from 0·43 to 1·89 for the second pair. The total luminance of the first pair averaged 1·90±0·08; the second pair averaged 2·10±0·22. Each observer received 25 presentations of all combinations for the first pair and 20 presentations of all combinations for the second pair. In half the presentations of the latter, the component colors to each eye were interchanged.

No "same" judgments were reported at either extreme of the first series. As the composition of the binocular stimulus matched the comparison field more closely, the frequency of "same" reports increased, but the distribution of judgments is not symmetrical about the mode. As shown in Fig. 4, binocular combinations containing a larger amount of BG than R are more frequently judged the same than combinations with larger amounts of R.

Similar results were obtained with the second pair of stimuli, as shown in Figs. 5 and 6. Again the "same" judgments occurred more frequently as the binocular stimulus became more like the comparison field and again the combinations containing a larger amount of B evoked the most responses. For this pair, however, observer S gave some "same" judgments for the extreme combinations.

A comparison of Fig. 5 with Fig. 6 shows the changes occurring when the binocular components are interchanged. The modal point for ES shifted toward the blue, while that for S shifted markedly toward the yellow.[2]

Although the exposure time in the latter half of the study was 15 sec, the observers responded as quickly as possible and their response times were recorded and showed there was no simple relationship between response time and frequency of matches. The stimulus series with the highest frequency of matches corresponded to a rather short average response time, approximately 8 sec. Indeed, all the series with a high frequency of matches had short response times. These times tended to increase as the frequency of matches decreased. This may, of course, simply represent the confidence with which the reports were made.

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DISCUSSION

These results show that binocular mixture of colors does not occur with every presentation. The frequency of such mixtures varies with the experimental conditions and the composition of the stimuli. Optimal conditions include a relatively long exposure time, a uniform surround, a small stimulus field and equal luminance of the two components; if the binocular stimulus is compared with a standard, the total luminance of both fields should be equal. If the conditions are not optimal, mixture will occur in fewer cases.

We have concluded that an "appropriate" exposure time is rather long, about 5 to 10 sec. If we must wait this long for the initial oscillation to cease before fusion occurs, does this indicate that no true mixture is taking place and that Helmholtz was correct in attributing the alleged mixtures to induction and afterimages etc.? We feel that such regularity of results as appears in Figs. 4, 5 and 6 argues against this interpretation. There does not seem to be any reason why small changes in the binocular components should affect the afterimages or the amount of background induction such that a greater frequency of matches would result. The marked relationship between the binocular composition and the frequency of matches in Figs. 4, 5 and 6 bespeaks actual color mixture. Since central processes are involved, long exposure times must be expected.

Our results indicate that, under certain conditions, the luminance of a binocular mixture may be the sum of its components. This has been a disputed point since FECHNER (1861) reported that if he placed a dark gray glass in front of one eye after looking at the sky with the other, the sky appeared darker when viewed binocularly. The effect of adding the reduced illumination to the one eye diminished the resultant total brightness. SHERRINGTON (1904–1905) subsequently found that monocular and binocular luminances were the same

[2] We have determined that the achromatic match point for S is considerably nearer the yellow region of the spectral locus than is the case for ES and, doubtless, these differences between observers and also between eyes are due, at least in part, to differences in macular pigmentation.

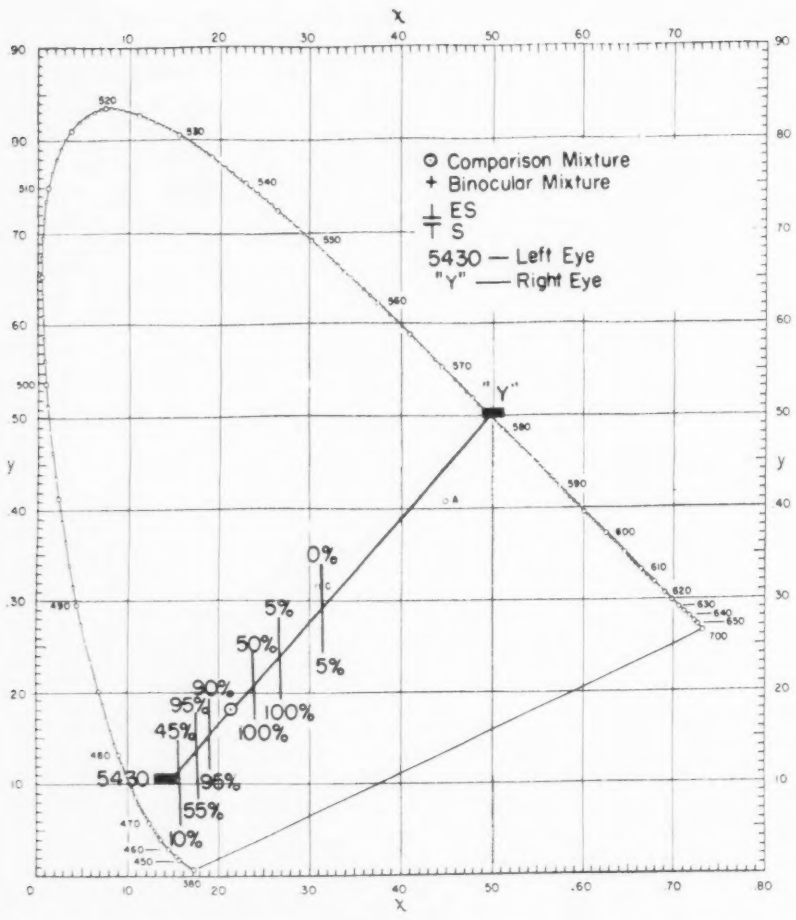

FIG. 6. The distribution of binocular match judgments. The per cent of "same" judgments for the same binocular mixtures as in Fig. 5 but with the components interchanged.

and concluded that there was little interaction between monocular and binocular vision. But BARTLEY (1941) criticized Sherrington's procedure and showed that monocular luminance is some value between equality and double that of the binocular luminance depending on the absolute luminance of the binocular field.

The present results show that the binocular mixture looked equal in brightness to the comparison (additive) mixture when the luminance of the binocular field equalled the luminance of either comparison field. That is, the total luminance of the two comparison fields was double the total luminance of the binocular fields. This appears to indicate that there is binocular summation of apparent brightness when the two fields are disparate but not when they are identical in hue.

The results in Part I, shown in Table 3, indicate that binocular mixtures with a red component required an excess of red to match the additive mixture. This supported Trendelenburg's results. But the results which are plotted in Figs. 4 and 5 indicate that less red was needed. The main difference between these two parts of the experiment is that in the

TABLE 3. FREQUENCY DISTRIBUTION OF JUDGMENTS FOR VARIOUS BINOCULAR COMBINATIONS

(a) Comparison field: 1·00 GY + 1·00 R

Binoc. comb.		Judgments									
GY	R	Same		Lighter		Darker		Oscillation		Dominance	
		S	ES	S	ES	S	ES	S	ES	S	ES
0·77	0·77		1			10	5		1		13
0·86	0·86	3	4			6	5	1	1		10
0·97	0·97	9	14				1	1			5
1·19	1·19	8	11		1			2	6		2
1·35	1·35							10	16		4

(b) Comparison field: 1·00 PB + 1·00 Y

0·54	0·54					10					10
0·72	0·72	5				5	10				
0·91	0·92	8	4			2	5		1		
1·03	1·04	10	9				1				
1·43	1·43			6				4	7		3
1·77	1·77			3				7	8		2

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former the luminance of the binocular field varied above and below the luminance of the comparison field. In the latter experiment, on the other hand, the two luminances were kept equal to each other. An explanation of the contradictory results may stem from a study of the red–green ratio as a function of luminance. DIMMICK and WIENKE (1958) have shown that the red–green ratio decreases as the luminance of the yellow standard increases. This decrease, furthermore, is not linear but is a negatively decelerating function. Thus, it follows that if, on the one hand, we have a red stimulus with a constant luminance and, on the other hand, a red stimulus whose luminance is varying about the comparison luminance, there will be an average net loss of its luminance in the latter case. The relative gain for the higher luminances will not completely offset the relative loss for the lower luminances. Thus we would expect to need an excess of red when the luminance of the stimulus is varied but not when it is constant.

CONCLUSIONS

1. The frequency of obtaining binocular color mixture varies with the experimental conditions and the composition of the stimuli.

2. Optimal conditions include an exposure time of 5 to 10 sec, a small stimulus field, uniform surrounds, and binocular components of equal luminance.

3. Binocular mixtures match an additive mixture with increasing frequency as the total binocular luminance is more closely equated to the additive luminance. When the binocular luminance is less than the additive luminance, there is a tendency for one of the binocular components to be dominant; when it is greater than the additive luminance, there are more reports of oscillation between the binocular components.

4. With the total binocular luminance equated to the additive luminance, but with variable binocular components, the greatest frequency of matches occurs when the two sets of components are comparable.

5. The luminance of a binocular mixture composed of two colors will match the luminance of the monocular mixture of these colors presented to one eye, but not the sum of the luminances of two such mixtures, one presented to each eye.

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AREA AND LUMINANCE OF TEST OBJECT AS VARIABLES IN EXAMINATION OF THE VISUAL FIELD BY PROJECTION PERIMETRY[1]

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Abstract—A modified Goldmann perimeter is used which provides means of measuring, in any desired location in the field, the luminance of the projected test object which is just perceptibly brighter than a background of fixed luminance.

Data for normal eyes are presented to show the relationship between area and threshold luminance and the variation in this relation from center to periphery of the retina. Similar tests of eyes having defects in the visual field provide a measure of the extent and density of the defect and a direct test for abnormality in the capacity for areal summation.

Résumé—Un périmètre modifié de Goldmann a donné la possibilité de mesurer, dans toutes les parties du champ, la luminance du test projeté qui est perçu comme tout juste plus brillant que le fond de luminance fixe.

Les données sont présentées pour des yeux normaux, afin d'établir la relation entre la surface et le seuil de luminance et la variation de cette relation à partir du centre jusqu'à la périphérie. Des tests analogues pour des yeux ayant des défauts dans le champ visuel donnent le moyen de mesurer l'étendue et l'importance du défaut et constituent une méthode directe de détection des troubles sommatifs.

Zusammenfassung—Ein modifiziertes Goldmann-Adaptometer, das die Möglichkeit gibt, im ganzen Gesichtsfeld die Leuchtdichte des projektierten Testobjektes (das kaum heller ist als der Hintergrund) genau einzustellen und zu messen, wurde benutzt.

Es werden Ergebnisse für normale Augen gewonnen, um die Verhältnisse zwischen Flächenausdehnung und Leuchtdichteschwelle und die Veränderung dieser Zusammenhänge zwischen Zentrum und Peripherie zu zeigen. Untersuchungen im Gesichtsfeld fehlerhafter Augen gestatten die Grösse und Zahl der Fehlreaktionen zu bestimmen und bilden direkte Teste für anormale Flächensummationen.

1. INTRODUCTION

THE GOLDMANN projection perimeter (1945a, b) provides for precise and reproducible gradations in the visibility of the test object, by variation of either its area or its contrast with the background or by a combination of both methods. There is need for further investigation in order to choose from the many possible sizes and luminances of test object viewed against a background of constant luminance those most useful in clinical perimetry. It is important, for example, to know whether early field defects are best detected by test objects of small size and relatively high luminance or by larger sizes of lower luminance. DUBOIS-POULSEN (1952) believes that in some forms of ocular pathology reduction in size is more

[1] From the Wilmer Ophthalmological Institute of The Johns Hopkins University and Hospital. This investigation was supported by Grant B-810 from the National Institutes of Neurological Diseases and Blindness, Public Health Service.

efficient in detecting early field changes than an equivalent (for the normal eye) reduction in luminance. A possible disadvantage of small test objects, on the other hand, is that their visibility may be significantly influenced by uncorrected errors of refraction.

The present investigation is concerned primarily with a study of normal eyes, to determine the relationship between area and luminance of a just perceptible test object and the variation in this relation from center to periphery of the retina. Data are also given for a few eyes with defects in the visual field. A later paper will present more extensive data on eyes with various forms of pathology affecting the visual field.

The procedure used in these studies has been variously designated as light-sense perimetry (SLOAN, 1939), quantitative perimetry (BAIR, 1940; HARMS, 1952) and static perimetry (FANKHAUSER and SCHMIDT, 1958). It differs from conventional perimetry with moving test objects (topographical perimetry, BAIR, 1940; HARMS, 1952; kinetic perimetry, FANKHAUSER and SCHMIDT, 1958), in that light thresholds are measured directly, at a series of fixed locations in the visual field, by varying the luminance of the test object. In conventional kinetic perimetry the visual field is explored with a moving test object of fixed luminance in order to locate points at which this luminance approaches the threshold value. Threshold measurements made by kinetic perimetry cannot be as precise and reproducible as those made by static perimetry because the rate at which the test object is moved and the promptness with which the subject reports its appearance or disappearance introduce unavoidable variations in the findings. The principal reason for using location of the test object as the variable, rather than luminance, is that exploration of the entire field of vision from center to periphery in a number of different meridians is less time-consuming by kinetic perimetry. In clinical studies static perimetry in a limited area of the field can nevertheless be a valuable supplement to the conventional method, for example in obtaining a precise measure of the density of a scotoma previously located by the kinetic method. Static perimetry may also detect early defects not revealed by kinetic perimetry (HARMS, 1952, 1957; WEEKERS and LAVERGNE, 1958). In this study the relationships between area and threshold luminance of a test object on a background of constant luminance are studied by the method of static perimetry because of the greater accuracy of this method. The findings are applicable to both static and kinetic perimetry.

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2. PREVIOUS INVESTIGATIONS

There are many basic studies in which the relationship between L, the light threshold, and A, the solid angle subtended by the test patch, is determined for some particular set of experimental conditions. Generally an attempt is made to fit the data to an equation of the form

$$\log L + k \log A = c$$

The coefficient k is sometimes referred to as the summation coefficient because it measures the additive effect of stimuli from contiguous areas of the retina. When there is complete spatial summation, and the threshold therefore depends only on the total amount of light in the test patch, k is equal to unity. When spatial summation is nil, and there is therefore no change in the threshold with change in area, k equals zero. For partial summation (the usual finding) k has some value between unity and zero. A majority of the previous investigations of area–luminance relationships are not closely related to perimetric studies, either because they apply only to the foveal region or because they concern the absolute rather than the differential threshold. Studies which provide information directly applicable to projection perimetry are those of GOLDMANN (1945a), DUBOIS-POULSEN and MAGIS (1957) and

FANKHAUSER and SCHMIDT (1958). Goldmann used conventional perimetry with moving test objects to find the changes in area and in luminance of the projected test object which would produce approximately the same alteration in the limits of the visual field. His data indicate, for example, that between test objects I and II (areas 1/4 and 1 mm²) there is partial summation such that the fourfold increase in area is approximately equivalent to an increase of luminance by a factor of 3·16. This corresponds to a summation coefficient of about 0·8 (log 3·16/log 4·0). The coefficient was found to be less for larger target areas. Its value also differed in different regions of the visual field. Goldmann concluded, however, that for purposes of clinical perimetry a constant summation coefficient of about 0·8 could be assumed. To correspond with this, the six test objects of the standard Goldmann perimeter have areas which differ by 0·6 in log units (i.e. they increase by a factor of 4) whereas the four standard luminances of test objects differ by 0·5 in log units. In retinal regions in which the relationship $\log L + 5/6 \log A = c$ holds good a test object of luminance 100 ml and area 1/4 mm², for example, should give the same isopter as one of luminance 10 ml, area 4 mm².

DUBOIS-POULSEN and MAGIS (1957) used the Goldmann instrument and the method of static perimetry to obtain direct measures of threshold luminance for five sizes of test field. They found an average summation coefficient of 0·962 for five trained subjects and 0·818 for sixteen untrained subjects. These investigators do not mention what retinal regions were studied except to say that locations within 10° of the fixation point were not tested.

FANKHAUSER and SCHMIDT (1958) emphasized the importance of knowing whether, in the normal eye, there is an exact or only an approximate constancy of the summation coefficient. This information has a definite bearing on findings of DUBOIS-POULSEN (1952, 1957) which seem to indicate that summation is abnormally high in patients with certain forms of ocular disease. In many of the visual fields shown in DUBOIS-POULSEN's textbook (1952), pairs of test objects assumed to be "equivalent" give wider fields for the dimmer and larger test object than for the brighter and smaller one. According to Dubois-Poulsen this type of finding indicates a disorder of spatial summation. Fankhauser and Schmidt used the methods of both static and kinetic perimetry to investigate the supposed constancy of summation throughout the retina of the normal eye. They used the five standard test objects of the Goldmann perimeter, which range in size from 1/4 to 64 mm². (Data for the 1/16 mm² test object were not included because of a question as to whether the specified area was actually produced.) The results are presented graphically in the form of threshold gradients showing, for each size, the change in log-threshold from center to periphery of the horizontal meridian. The fact that the vertical separation on the log-luminance coordinate of the gradients for different sizes is not constant but increases with increasing distance from the fovea shows that summation also increases gradually from center to periphery of the field. Lack of perfect coincidence of supposedly equivalent isopters on the Goldmann perimeter is therefore not necessarily evidence of an abnormality of spatial summation. FANKHAUSER and SCHMIDT (1958) conclude that further data are needed to establish the summation characteristics of the normal eye, and that static perimetry is the preferred method of investigation.

3. EQUIPMENT

The data to be reported in this paper were obtained with a Goldmann Spherical Projection Perimeter provided with several items of accessory equipment to permit measurement of the differential threshold in any location of the visual field including the fovea. With one exception these accessories were supplied by the firm of Haag-Streit, manufacturers of the Goldmann perimeter.

TABLE 1. GRADATION OF SIZES OF OVAL TEST OBJECTS OF GOLDMANN PERIMETER

Arbitrary designation	Area (mm²)	Log area	Conventional notation for circular test objects of about the same angular size	
V	64	1·8	30/1000	10/330
IV	16	1·2	15/1000	5/330
III	4	0·6	7·5/1000	2·5/330
II	1	0·0	3·7/1000	1·2/330
I	1/4	−0·6	1·8/1000	0·6/330
0	1/16	−1·2	0·9/1000	0·3/330

Table 1 gives data on the sizes of the six test objects. Column 1 gives the arbitrary designations in roman numerals used by Goldmann, column 2 gives the areas in square millimetres of the oval test objects, column 3 the logarithms of these areas. Columns 4 and 5 give, for orientation, the conventional notations for circular test objects of approximately the same solid visual angle when viewed from distances of 1 m and 33 cm. It may be seen from the table that the smallest Goldmann test target is approximately equivalent to a 1 mm circular target at a distance of 1 m and the largest is approximately equivalent in angular size to a 10 mm circular target at a distance of 33 cm.

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Fig. 1 shows the equipment for holding the projected test spot at any desired location. In the photograph the regulating device is in position for making measurements from center to periphery in an oblique meridian. A voltage regulator, a variable rheostat in series with the perimeter lamp and a small luxmeter are used to secure and maintain the desired maximal luminance of the test object (100 ml, i.e. 2·0 log ml, in this study). A third modification of the standard instrument is the addition of supplementary neutral filters to provide for a decrease in luminance of the test object over a range of 4 log units in steps of 0·1 log unit. The filters of the standard instrument have densities of 0·0, 0·5, 1·0 and 1·5 and provide therefore luminances of 2·0, 1·5, 1·0 and 0·5 log ml (in arithmetic units 100, 31·6, 10 and 3·16 ml). In our modified instrument a second series of five neutral filters, with densities of 0·0, 0·1, 0·2, 0·3, 0·4 (see Fig. 2), provides for variation in the luminance of the test spot in steps of 0·1 log unit. A filter cap of density 2·0 may be placed over the projector to extend the range of luminances down to −1·5 log ml (0·0316 ml). The luminance of the background is controlled, as in the standard Goldmann perimeter, by matching it to the projected test object at some chosen level. In this investigation the standard background luminance of 3·16 ml (0·5 log ml) was used. The fourth accessory is a projected pericentral target for controlling fixation when threshold measurements are made at the fovea. The target supplied by Haag-Streit for monocular control of fixation consists of four spots at the corners of an imaginary square whose sides subtend a visual angle of about one degree. In preliminary studies we found that these four spots could not always be seen by the patient with a central scotoma. The much larger binocular pericentral fixation targets supplied with the standard Goldmann perimeter on the other hand proved unsatisfactory for many normal subjects because of fixation disparity. The monocular fixation target employed in this study, a circle of 10° diameter with four obliquely located radii, has for many years been used in this laboratory on our tangent screens and has proved very successful in securing central and steady fixation from patients with scotomas or other field defects involving the fovea. In

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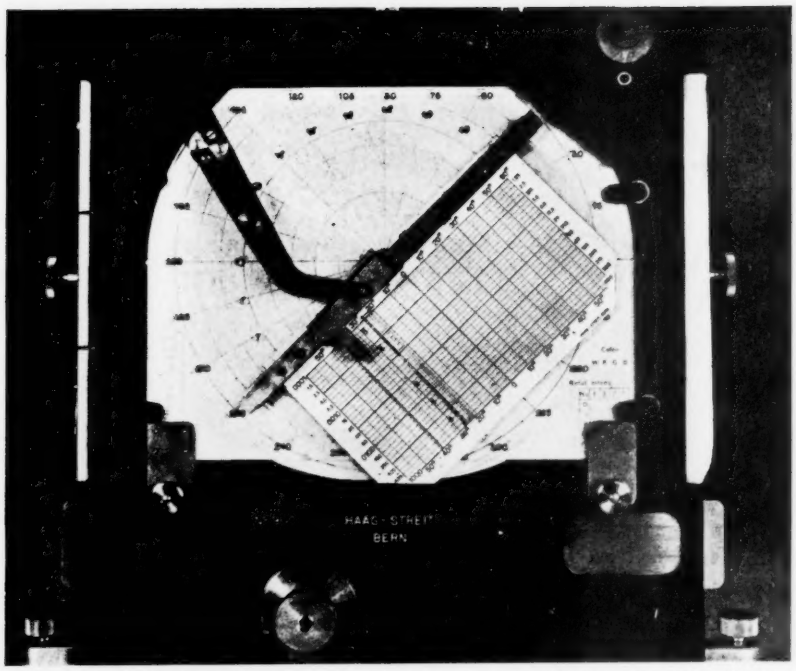

FIG. 1. Special device for placing the projected test spot in any desired location of the visual field. The regulating device is shown in position for making measurements in an oblique meridian.

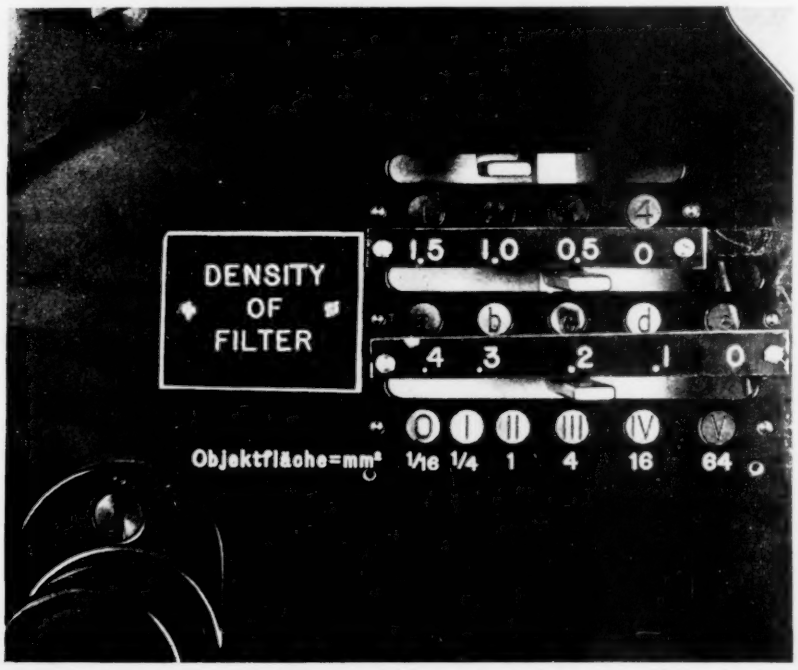

FIG. 2. Showing control panel with levers used to vary luminance and size of test object. The photograph shows the levers of the first and second row set so that the density of the filters totals 1·2. The lever of the third row is set to give a test object of 4 mm² (size III).

[*facing p.* 124]

FIG. 3. Monocular pericentral fixation target used in measuring fovea thresholds.

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adapting this type of target to the Goldmann perimeter we did not attempt to correct for the slight distortion of the projected circular target (see Fig. 3).

4. GRAPHICAL PRESENTATION OF DATA

Three types of graph are used in this study to demonstrate the interrelationships between the minimum perceptible luminance of the test object, its area, and its location in the visual field. The first type shows the decrease in threshold luminance, L, with increase in area, A, for a specific retinal location. Values of A in logarithmic units are represented on the abscissa, the corresponding values[2] of log L on the ordinate. These graphs will be referred to hereafter as summation graphs.[3]

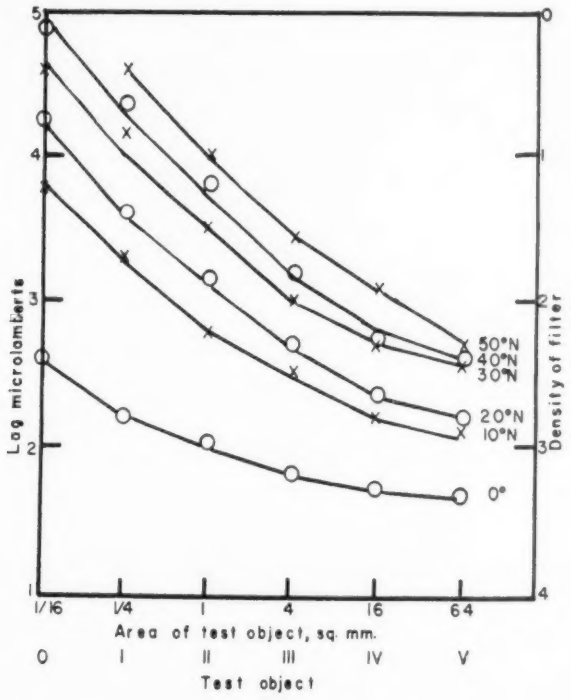

FIG. 4. Summation curves of a normal subject, L.S., for the fovea and for various locations in the nasal field.

The second type of graph shows the variation in log L with retinal location for a specific size of test object. Distance in degrees from fixation for a given meridian of the visual field is represented on the abscissa, the corresponding value of log L on the ordinate. These graphs will be referred to as threshold gradients.

The third type of graph is a conventional perimetric chart, and shows for any given size and luminance of test object the location in each meridian at which it is just perceptible. The

[2] The microlambert (μL) is taken as the unit to avoid negative values of log L. One millilambert (mL) equals 1000 μL. One apostilb equals 100 μL.

[3] This designation is not intended to rule out the possibility that the area-luminance relationships are determined by both summative and inhibitory mechanisms.

line connecting the series of threshold locations is commonly designated an isopter. In this study the data for plotting the isopters are derived from the threshold gradients measured in horizontal, vertical and oblique meridians of the visual field. Such derived isopters, based on the technique of static perimetry, can be more precisely determined than those obtained by conventional kinetic perimetry. They provide therefore a more reliable basis for testing the equivalence of different combinations of size and luminance.

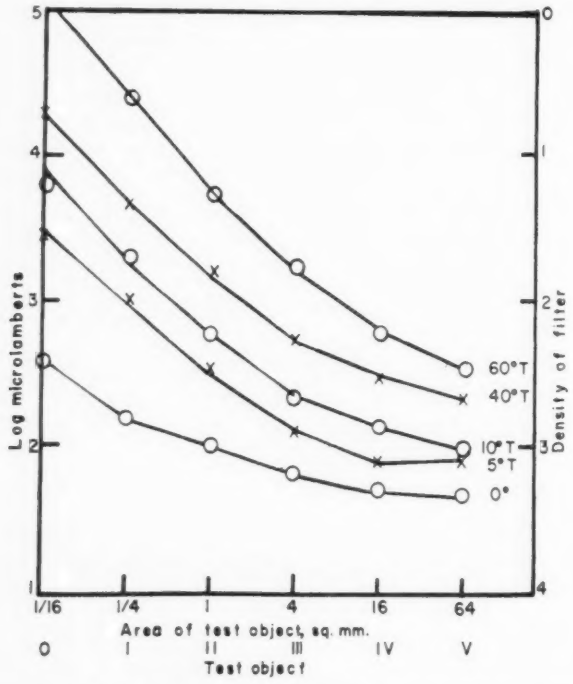

FIG. 5. Summation curves of a normal subject, L.S., for the fovea and for various locations in the temporal field.

5. RESULTS

A. Summation Graphs

Figs. 4 and 5 show for a normal subject (L.S.) summation graphs for the fovea and for a series of locations in the horizontal meridian extending to 50° nasally and to 60° temporally. None of the data for this normal eye fits the linear relationship between log A and log L assumed by Goldmann in selecting his equivalent test objects. Instead, the curvilinear graphs show a regular decrease in slope with increasing area of the test object. The decrease in threshold luminance with increase in area is least at the fovea and increases toward the periphery. If the two larger sizes of test object are omitted, the data for retinal locations 30° or more from fixation can be fitted approximately to straight lines corresponding to the equation $\log A + k \log I = c$. This is shown in Fig. 6 where best fitting straight lines have been drawn through points corresponding to the experimentally determined thresholds at 30°, 40°, 50° and 60° in the temporal field and at 30°, 40° and 50° in the nasal field. The slopes of these lines correspond to values of k ranging from 0·87 to 1·00. Data for the more central regions of the retina cannot be closely fitted to straight lines except for a restricted range of

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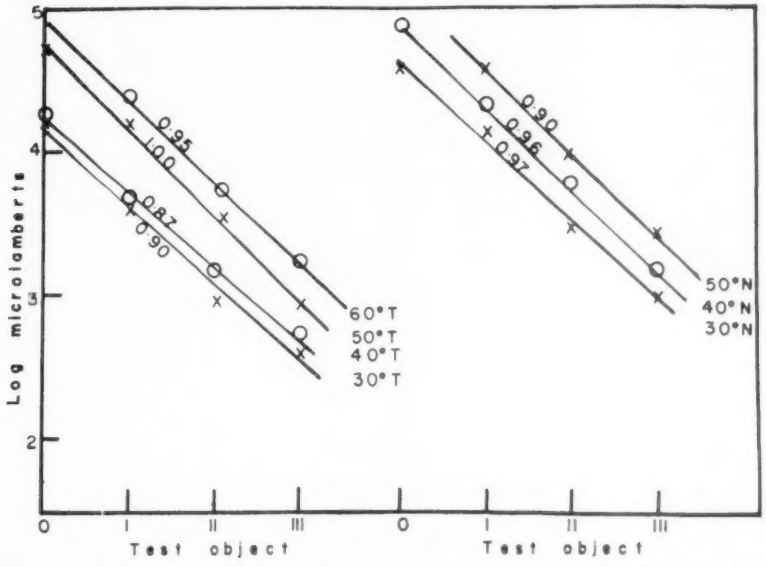

FIG. 6. To show that for test objects of size III and smaller, in the periphery, the relationship between area and threshold luminance can be expressed by the equation $\log L + k \log A = C$. The numerical value of the summation coefficient, k, is shown above each curve.

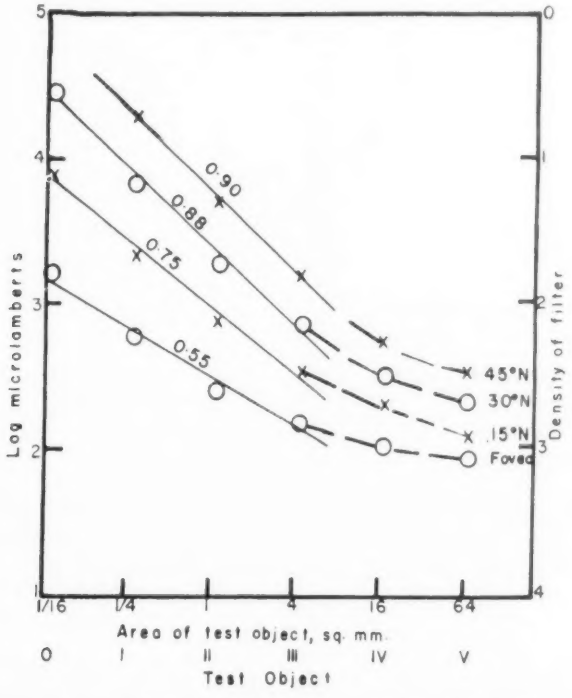

FIG. 7. The average summation graph of a group of normal eyes, for the fovea and for various locations in the nasal field. The value of the summation coefficient, k, is shown above each curve.

sizes of test object. In any such limited range the slope of the line is significantly less than the value of 0·8 adopted by GOLDMANN (1945) as an average applicable to the entire field.

To see if the data for observer L.S. are typical of normal subjects in general the summation curves of from ten to twenty normal eyes were measured at the fovea and at 15°, 30° and 45° in the nasal field.[4] These curves also show a gradual increase in the capacity for summation with increasing distance from the fovea. The mean summation graphs for each location are shown in Fig. 7. Best fitting straight lines have been drawn through the points

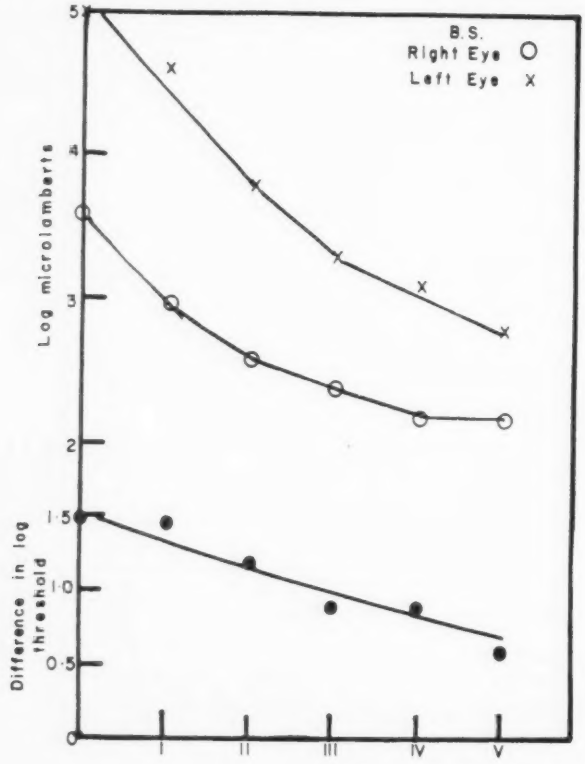

FIG. 8. The two upper curves show the summation graphs, at 2° nasal, of B.S., a patient with papilloedema of the left eye and a normal right eye. The lower graph shows the increase in thresholds of his affected left eye relative to those of his normal right eye.

Case 1, B.S. This patient has in the left eye a marked papilloedema. The large scotoma centered on the normal blind spot extends slightly beyond the fovea into the nasal field. The corrected vision of this eye is 20/25; that of the normal right eye is 20/15. Summation curves were determined at 2° from fixation in the nasal field. The thresholds of the left eye are, for all six test objects, significantly higher than those of the normal right eye. The left eye also shows a relatively greater decrease in threshold with increase in area.[5] This is indicated more clearly in the lower section of Fig. 8 which shows for each size of test object the difference in the thresholds of the two eyes.

[4] The ten or more subjects tested at each of the four locations are, with a few exceptions, not the same individuals.

[5] It is difficult to understand how retinal or other ocular pathology could result in an *increase* in the capacity for areal summation. The area–luminance relationship may, however, depend in part upon inhibitory mechanisms. Impairment of the normal inhibitory processes as a result of retinal disease could account for an apparent increase in the capacity for summation.

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corresponding to the thresholds for test objects of size III (4 mm²) and smaller. The values of the summation coefficient k, determined by the slopes of these lines, increase from center to periphery. At the fovea and at 15° in the nasal field k is less than 0·8, the value assumed by Goldmann; at 30° and 45° it is greater.

These findings are in agreement with those of FANKHAUSER and SCHMIDT (1958) in showing that, in the normal eye, summation is not constant throughout the retina, as is assumed in the selection of equivalent test objects on the Goldmann perimeter. A defect in the visual field, when associated with lack of coincidence of the isopters of supposedly equivalent test objects, does not necessarily indicate a concomitant disorder of the summation mechanism. A direct and unequivocal test for such an abnormality can be obtained

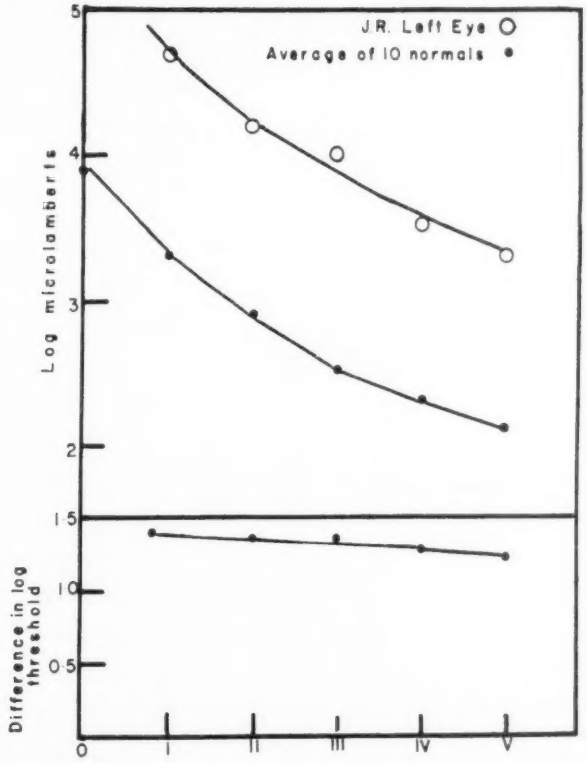

FIG. 9. The two upper curves show summation graphs, at 15° nasal, of J.R., a patient with pigmentary degeneration of the retina and, for comparison, the average summation graph of ten normal eyes. The lower graph shows the increase in log thresholds of J.R. relative to those of the average normal eye.

Case 2, J.R. This patient has pigmentary degeneration of the retina with ring scotomas in each eye for a 3/330 white test object.[6] Fig. 9 shows the summation curve of the left eye measured in the horizontal meridian at 15° from fixation in the nasal field. The figure also shows for comparison a normal summation curve for this region. The lower section of the graph shows the amount by which the patient's thresholds differ from the normal values. The increase in threshold is only slightly greater for small than for large test objects. In this case, therefore, there is no evidence of a significant abnormality in the capacity for areal summation, such as was noted in the patient with papilloedema.

[6] Additional data on this patient are given in a later section.

by measuring the summation graph in a region of the field showing impaired sensitivity and comparing it with a normal graph for the same region. If the defect in the field is unilateral a summation graph of the other eye, measured in the appropriate location, provides the ideal standard of comparison. Figs. 8 and 9 illustrate the procedure. More extensive clinical data of this sort will be reported in a later paper.

Further study of summation curves to determine whether specific diseases are associated with an abnormal area–luminance relationship might contribute information of great theoretical interest in a study of retinal mechanisms for areal summation and inhibition. The results of such tests also have a bearing on the practical problem of selecting the most

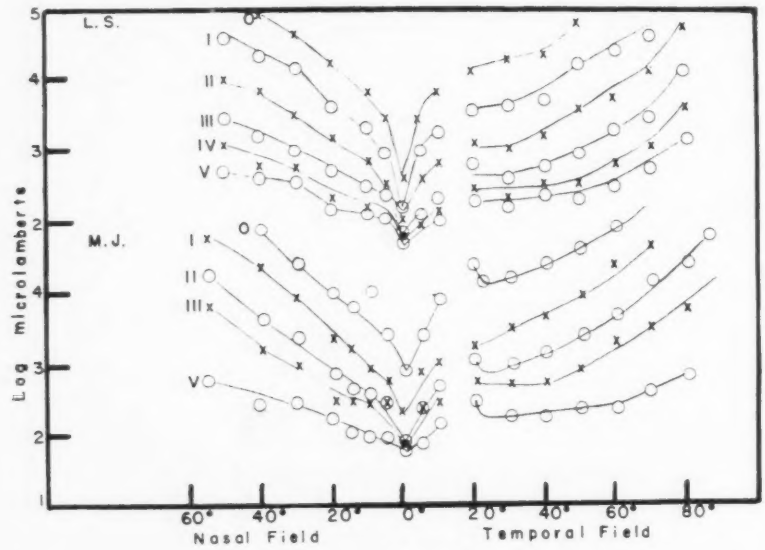

FIG. 10. Threshold gradients of two normal subjects (L.S. and M.J.) in the horizontal meridian. The size of the test object is shown at the left of each curve.

suitable sizes and luminances of test object to detect early field defects. If, as is suggested by the findings of DUBOIS-POULSEN (1952, 1957), in some forms of ocular disease the increase in threshold is consistently greater for small than for large test objects, it provides one argument in favor of decreasing the visibility of the test object by reduction in its size rather than in its luminance. As will be seen in the next section, however, other considerations argue against the use of very small test objects.

B. Gradients of Threshold Luminance

(1) Threshold gradient of normal eye. Fig. 10 shows for two normal observers (L.S. and M.J.) the variation in threshold luminance in the horizontal meridian. The curves for the different sizes of test object all show a regular increase in threshold from center to periphery. The rate of increase is very gradual for the largest test object and increases with decrease in area of test object. The differences in shape of the different gradients provide another demonstration of the fact that the area–luminance relationship varies with retinal location.

Fig. 11 demonstrates in another way the increase in areal summation associated with increased distance from the fovea. This figure gives for each location in the horizontal

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meridian the difference in log threshold for test object 0 (1/16 mm²) and for test object III (4 mm²). If there were complete areal summation this increase in area of 1·8 log units would be associated with an equal decrease in threshold luminance of 1·8 log units. The actual difference in luminance is about 0·9 log units at the fovea, increases gradually toward the periphery and approaches the value of 1·8 corresponding to complete summation at about 60° in the temporal field and 50° in the nasal field.

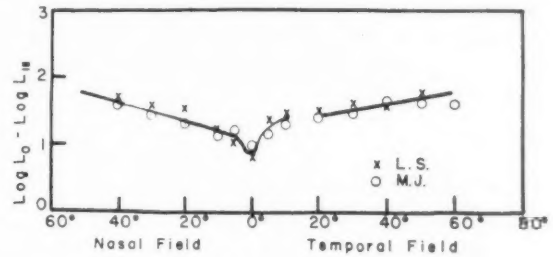

FIG. 11. Increase in log threshold with decrease in area from 4 mm² (size III) to 1/16 mm² (size 0). The data are for the horizontal meridian.

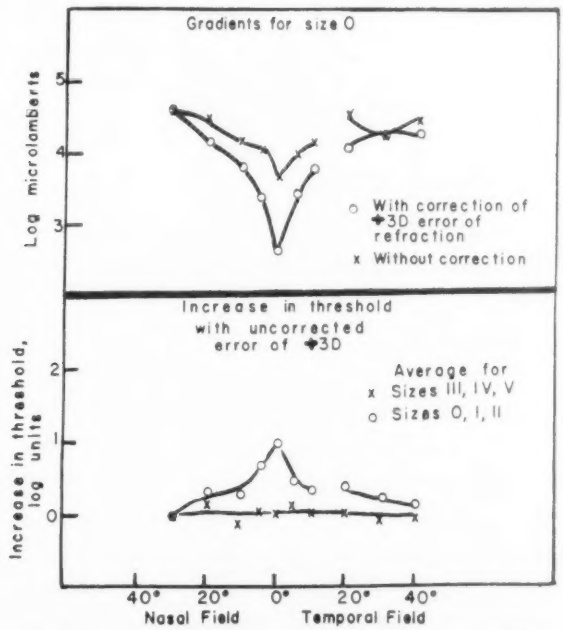
Gradients for size 0
Log microlamberts
o With correction of +3D error of refraction
x Without correction
Increase in threshold with uncorrected error of +3D
Increase in threshold, log units
Average for
x Sizes III, IV, V
o Sizes 0, I, II
40° 20° 0° 20° 40°
Nasal Field
Temporal Field

FIG. 12. The upper section of the graph shows the threshold gradients of a normal emmetropic eye for a test object of size 0, with and without the required + 3·00 diopter correction for presbyopia. The lower section shows, for large and small test objects, the increase in threshold with an uncorrected error of refraction of + 3·00 diopter.

The gradients of one normal subject (M.J.) for sizes 0, I, II and III were also measured in the vertical and in the two oblique meridians of the visual field. The results are essentially similar to those for the horizontal meridian. The rate of increase in threshold from center to periphery is more rapid for small than for large test objects and there is therefore increasing summation with increase in distance from the fovea.

(2) *Effect of uncorrected error of refraction on the gradient.* In choosing the most desirable size of test object for study of the visual field either by kinetic or by static perimetry, consideration must be given to the effect of an uncorrected error of refraction on the thresholds. Fig. 12 gives data on the threshold gradients of an emmetropic presbyopic eye with and without the required +3·00 diopter correction for the 30 cm distance of the test object. The upper graph shows the gradients of the horizontal meridian for the smallest of the Goldmann test objects. The increase in threshold resulting from the out-of-focus retinal image is greatest at the fovea, less in the paracentral regions and of negligible amount at 30° or more from fixation. Similar results were obtained with test objects I and II. With the

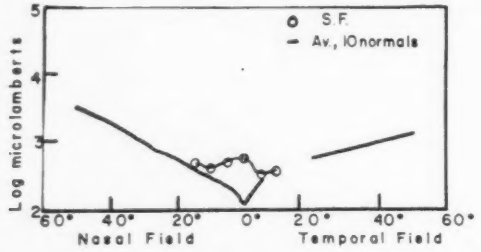

FIG. 13. Threshold gradient of S.F., a patient with central serous retinopathy, and average gradient of ten normal eyes. Test object, size III; horizontal meridian.

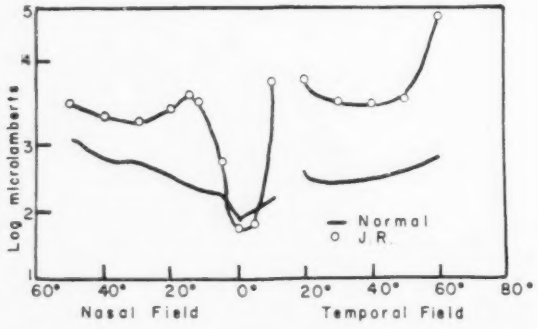

FIG. 14. Threshold gradients of J.R., a patient with early pigmentary degeneration of the retina, and of two normal eyes. Test object, size IV; horizontal meridian.

Case 3, S.F. The data for this patient illustrate the use of threshold measurements in establishing the extent and density of a central scotoma. The right eye has a central serous retinopathy and a corrected visual acuity of 20/25. A 6/330 blue test object is seen as green in a central area of the field about 10° in diameter. No definite scotoma could be mapped with any white test object. Fig. 13 shows the threshold gradient for a size III test object in the central portion of the horizontal meridian. The average gradient for ten normal eyes is also shown. The patient's gradient reveals a localized elevation of the thresholds limited to the fovea and immediately surrounding regions. At 10° in the nasal field and at 5° in the temporal field the thresholds are close to the average normal values.

Case 2, J.R. Data for this patient illustrate the value of the threshold gradient in study of the field defect associated with an early pigmentary degeneration of the retina. Fig. 14 shows the gradient of the left eye for a size IV test object and for comparison the average gradient of two normal subjects. Except in a central area extending from about 7° in the temporal field to 4° in the nasal field, all of the patient's thresholds are higher than normal. The abrupt rise in threshold at 5° to 10° from fixation in the nasal and temporal fields corresponds approximately to the inner border of the ring scotoma for a 3/330 white test object detected by a conventional perimetric examination. The visual field for this test object, shown in Fig. 15, gives however little indication of the widespread involvement of the field that is suggested by the threshold gradient.

three larger sizes, on the other hand, the +3·00 diopter error of refraction had no significant effect on the threshold even at the fovea. The average change for the three smaller and for the three larger test objects is shown in the lower graph of Fig. 12. The findings indicate that when test objects of size II or smaller are used to determine a threshold gradient, glasses correcting any significant error of refraction for a distance of 30 cm should be worn for measurements within 20° from the center of the field. If the subject's error of refraction is not known it is best to use a test object of size III or larger to study the central visual field.

(*3*) *Threshold gradient as a measure of the density and extent of a defect in the visual field.* When there is a scotoma or other localized field defect, determination of a threshold gradient in an appropriate meridian can be of value as a supplement to and confirmation of the findings of kinetic perimetry. Comparison of the gradient with that of the normal eye provides a measure of the density and extent of the defect.

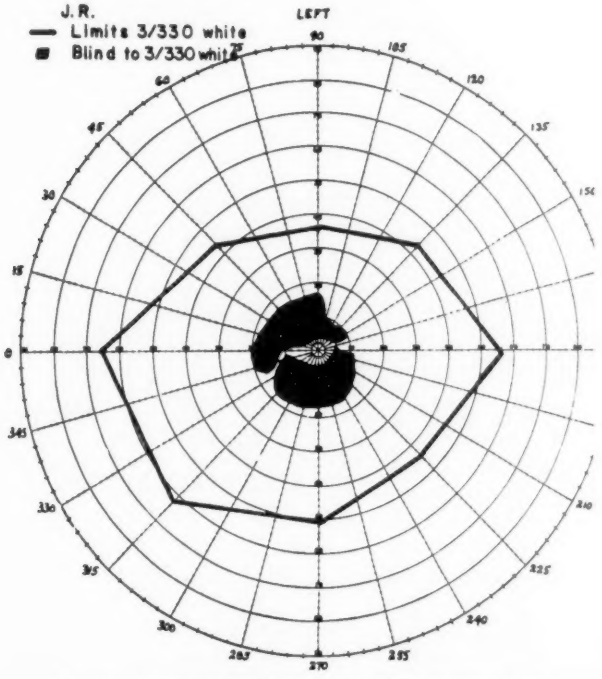

FIG. 15. Visual field of J.R. for 3/330 white test object.

(*4*) *Relationship between threshold gradients and isopters.* Threshold gradients of the normal eye provide information of value in selecting a graduated series of test objects for examination of the field by kinetic perimetry. More than twenty years ago BAIR (1940) pointed out that when there is a steep gradient for a graduated series of test objects their isopters will be close together; with a flatter gradient they will be spread apart. According to BAIR, widely spaced isopters are preferable because "the closer together the normal isopters the smaller is the zone of the field that can be examined by a given test object with reasonable delicacy". Gradients that are almost flat in certain regions such as, for example, those shown in Fig. 10 for test object V (64 mm^2) are however not as desirable

for kinetic perimetry as is a gradient with a moderate regular increase in threshold from center to periphery. With a very flat gradient, slight changes in luminance either of the test object or its background, or minor fluctuations in retinal sensitivity of no clinical significance may result in marked variations in the limits of the field for a given test object.

From a series of threshold gradients in different meridians it is possible to determine graphically the limits of the field for any given size and luminance of test object. These data provide therefore an indirect method of determining the isopters for any selection of test objects graduated either in size or in luminance. Various isopters derived from the threshold gradients of subject M.J. are presented in the next section.

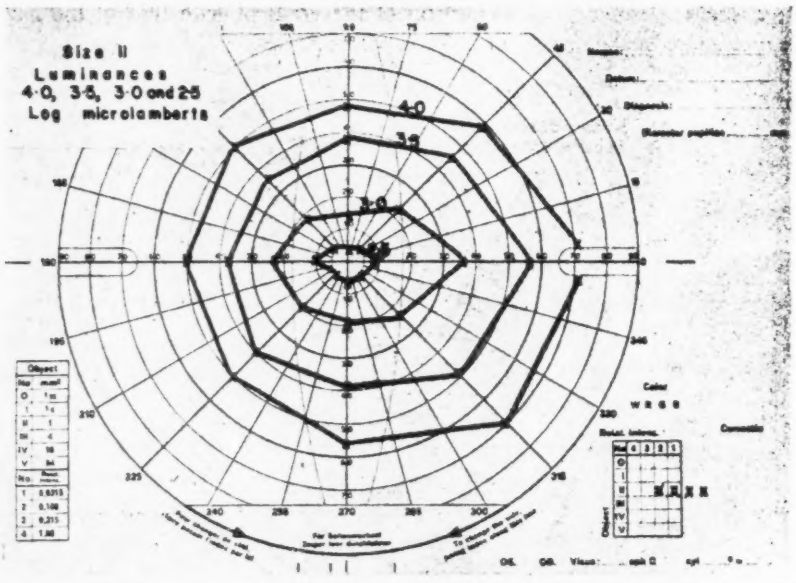

FIG. 16. Isopters of a normal subject (M.J.) for a test object of size II (1 mm²). The luminances are 4·0, 3·5, 3·0 and 2·5 log μL.

C. Isopters Derived from Threshold Gradients of a Normal Eye

Fig. 16 shows for subject M.J. the limits of the visual field for four different test objects, all of size II, whose luminances in log μL[7] are 4·0, 3·5, 3·0 and 2·5.

A similar distribution of isopters can be obtained by suitable selection of test objects which are of the same luminance and differ only in area. This is demonstrated in Fig. 17 which shows, for the same normal eye, the limits of the field for test objects of size 0, I, II and III (1/16, 1/4, 1 and 4 mm²), all of which have the same luminance (3·5 log μL). It is apparent from inspection of the graphs that examination of the visual field with either of these two sets of graduated test objects should detect impaired sensitivity in any region of the field from center to periphery.

DUBOIS-POULSEN (1952, 1957) believes that a variation both in size and in luminance of the test objects can provide useful information as to the normality of the area–luminance

[7] The luminances of the test objects of the standard Goldmann perimeter expressed in these units are 5·0, 4·5, 4·0 and 3·5. In this study luminances below 3·5 were obtained by means of the auxiliary filter described previously.

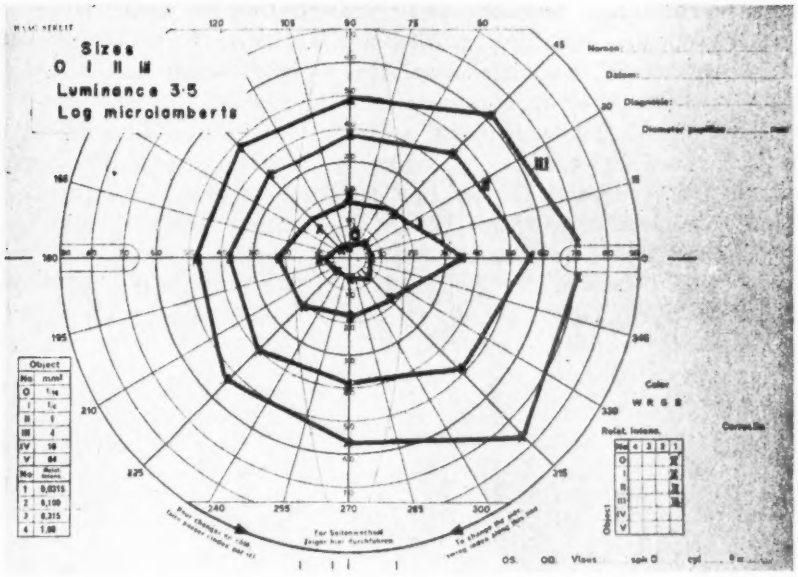

FIG. 17. Isopters of a normal subject (M.J.) for four sizes of a test object of luminance 3·5 log μL. The sizes are 0, I, II and III (1/16, 1/4, 1 and 4 mm^2).

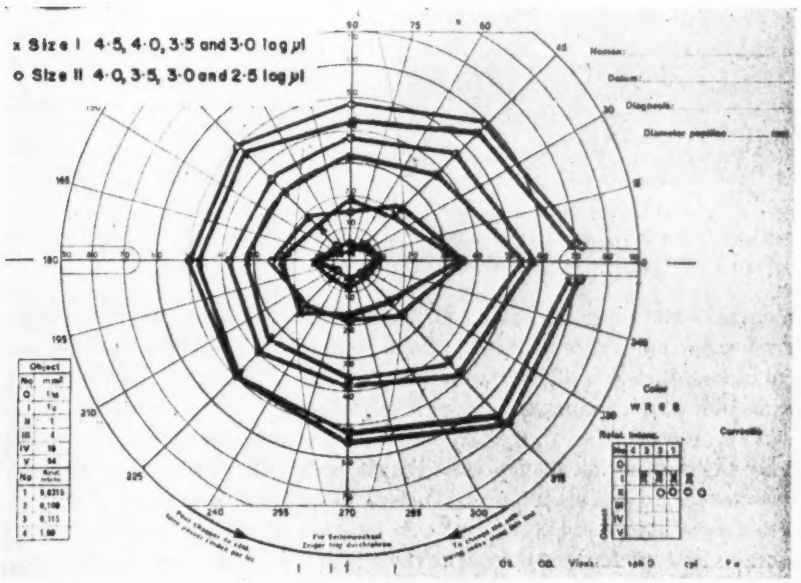

FIG. 18. Isopters of a normal subject (M.J.) for four pairs of test objects, which are equivalent according to the Goldmann assumption that a 0·6 decrease in log area is compensated by a 0·5 increase in log luminance.

relationship. His test for abnormality in the capacity for areal summation is based on acceptance of the Goldmann assumption that variation in steps of 0·6 in log area is equivalent to variation in steps of 0·5 in log luminance. This corresponds to a summation coefficient, k, equal to 5/6. It has, however, been amply demonstrated earlier in this paper that summation is by no means constant in different retinal areas of the normal eye. Deviation from perfect coincidence of the isopters of "equivalent" test objects is therefore to be expected as a general rule. This is illustrated in Fig. 18 which shows, for subject M.J., the isopters for four pairs of "equivalent" test objects. The test objects of size I (1/4 mm²) have luminances of 4·5, 4·0, 3·5 and 3·0 log μL. The four "equivalent" test objects of size II (1 mm²) have luminances of 4·0, 3·5, 3·0 and 2·5 log μL respectively. In the case of the isopters falling in the more peripheral regions of the field, size II gives in each meridian significantly wider

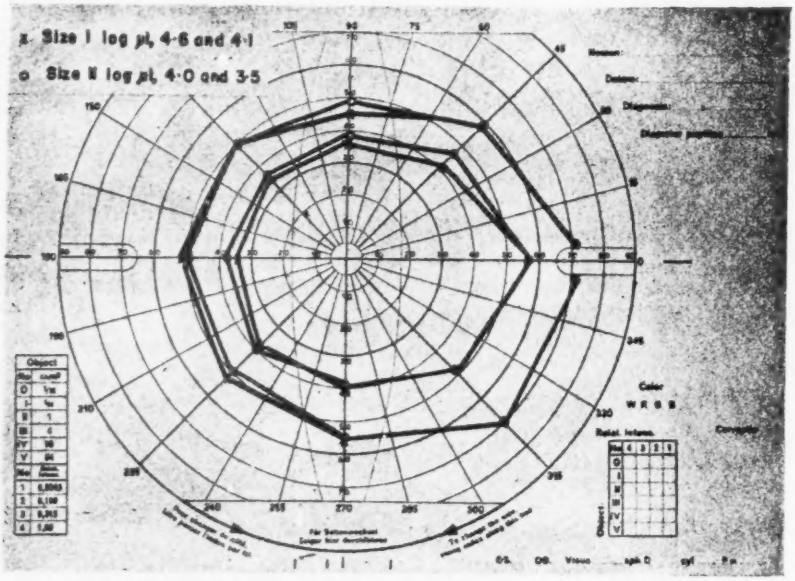

FIG. 19. Isopters for test objects of sizes I and II (1/4 and 1 mm²). The luminances of the smaller test object are four times those of the larger and should therefore be equivalent when there is complete areal summation.

limits than the "equivalent" test object of size I. The fact that the larger and dimmer test object gives wider limits than the smaller and brighter one indicates that the summation coefficient exceeds the value of 5/6 assumed in selecting the "equivalent" pairs of test objects.

If we assume that summation is complete in the peripheral retina beyond 30° from fixation for test objects I and II, then truly equivalent luminances in these two sizes should differ by 0·6 log units rather than by 0·5. Fig. 19 shows, for subject M.J., isopters for test objects selected to test this assumption. Those of size II have luminances of 4·0 and 3·5 log μL; the corresponding test objects of size I have luminances of 4·6 and 4·1 log μL respectively. The deviations from perfect coincidence of the paired isopters are slight and do not indicate a consistent difference in the limits of the fields for the smaller and brighter test object and for the larger and dimmer one. The data are therefore consistent with the assumption that the summation coefficient, k, is not significantly different from unity.

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With a standard Goldmann perimeter it is possible to compare the isopters for pairs of "equivalent" test objects in any given area and for any range of sizes, to determine whether the summation coefficient, k, is equal to, greater than, or less than 5/6. There is, however, no simple relationship between the numerical values of k and the amount by which the isopters are separated. This separation depends in a complex manner upon the sizes of the test objects compared and upon the slope of the threshold gradient of each test object in the region investigated.

A majority of the visual fields in DUBOIS-POULSEN's book (1952) which are classified as showing a "*trouble sommatif*" have wider limits for the larger and dimmer of the pair of equivalent test objects, indicating that k is greater than 5/6. The data presented in Fig. 18 show that this type of "summation trouble" can also occur in a normal eye. It is therefore difficult to understand why it is observed so rarely by Dubois-Poulsen in association with lesions of the conducting pathways and so frequently in association with retinal lesions. Supplementary tests involving direct determination of summation graphs and threshold gradients in appropriate locations might provide an answer to this question.

VI. SUMMARY AND CONCLUSIONS

1. Modifications of the standard Goldmann perimeter are used which provide means of measuring, in any desired location of the visual field, the luminance of the projected test object which is just perceptibly brighter than a background of fixed luminance.

2. Data for normal eyes are presented to show the relationship between area, A, and luminance, L, of a just perceptible test object, and the variation in this relation from center to periphery of the retina. Summation graphs, showing the relationship between log A and log L, indicate that areal summation decreases with increase in the size of the test object and increases with increasing distance from the fovea.

3. The same data for normal eyes, plotted as threshold gradients, show for each size of test object the variation in log L with retinal location. The rate of increase in log L with increasing distance from the fovea is more rapid for small than for large test objects.

4. In an eye with a defect in the visual field, determination of the threshold gradient in an appropriate meridian provides a precise measure of the extent and the density of a localized field defect. Determination of a summation graph in an appropriate location provides a direct test for abnormality in the capacity for areal summation.

5. A graduated series of test objects suitable for examination of the entire field of vision by the method of kinetic perimetry can be obtained either by variation in size or in luminance. For example, a suitable series of sizes, all of luminance 3·5 log μL, are 1/16, 1/4, 1 and 4 mm^2. An approximately equivalent series, all one mm^2 in size, have luminances of 4·0, 3·5, 3·0 and 2·5 log μL.

Acknowledgement—I am indebted to MARIA JABLONSKI and DARLENE BROWN for assistance in collection of the data for this study.

Editor's note—The complete tables have been deposited as Document number 6531 with the ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington, D.C., U.S.A. Copies may be obtained by citing the Document number and by remitting $1·25 for either photoprints or 35 mm microfilm. Please make remittance payable to: Chief, Photoduplicating Service.

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THE ELECTRORETINOGRAM OF THE ANTELOPE GROUND SQUIRREL

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Abstract—The electroretinogram (ERG) of this ground squirrel, an animal with a pure-cone type of retina, was found to have a prominent *a*-wave, a relatively fast *b*-wave and no *c*-wave. The *d*-wave was also large and it showed the familiar dependency on duration of stimulation that is characteristic of off-effects. The key finding was the demonstration that the *b*-wave was duplex, consisting of two components (b_1, b_2) which were present in responses to flashes at all wavelengths from 454 mμ to 631 mμ. These two components showed independence in so far as their behavior to changes in light intensity and to light adaptation was concerned. The significance of this finding is that the human ERG also has two separate *b*-components which are usually assigned to separate activity in rods and cones. This cannot be the explanation for the two *b*-waves of the ground squirrel since only cones are present. Evidently a duplex *b*-system, behaving in some respects like the rod–cone system of the human retina, can occur in a retina with a single morphological type visual cell.

Résumé—L'électrorétinogramme (ERG) de cet écureuil terrestre, dont la rétine ne contient que des cônes, présente une onde *a* très marquée, une onde *b* relativement rapide et pas d'onde *c*. L'onde *d* est forte elle aussi et dépend de la durée du stimulus d'une façon qui est caractéristique des effets "off". Le résultat essentiel est la démonstration de la dualité de l'onde *b*, ses deux composantes (b_1, b_2) étant présentes dans les réponses à des éclairs de toutes longueurs d'onde depuis 454 jusqu'à 631 mμ. Ces deux composantes se comportent indépendamment vis à vis des changements d'intensité lumineuse et d'adaptation à la lumière. Ces résultats signifient que l'explication usuelle des deux composantes séparées de l'onde *b* de l'ERG humain, à savoir l'activité séparée des cônes et des bâtonnets, n'est pas fondée dans le cas de l'écureuil terrestre qui ne possède que des cônes. On en déduit qu'une dualité de l'onde *b*, provenant d'un système qui à certains points de vue fonctionne comme le système cône–bâtonnet de la rétine humaine, peut se manifester dans une rétine qui ne possède qu'un seul type morphologique de cellule visuelle.

Zusammenfassung—Das Elektroretinogramm dieses Boden-Eichhörnchens, eines Tieres mit einer reinen Zapfen-Netzhaut, hat eine ausgeprägte *a*-Welle, eine relativ schnelle *b*-Welle und keine *c*-Welle. Die *d*-Welle ist ebenfalls gross und zeigte die bekannte Abhängigkeit von der Reizdauer, die charakteristisch für "off"-Effekte ist. Das Hauptergebnis ist die Beobachtung, dass die *b*-Welle ein Dublett war, also aus zwei Teilen (b_1, b_2) bestand, die bei allen Reizen zwischen 454 bis 631 mμ auftreten. Die beiden Komponenten waren hinsichtlich ihres Verhaltens bei Änderung der Lichtintensität und -adaptation unabhängig. Das Bemerkenswerte an dieser Beobachtung besteht darin, dass das menschliche ERG ebenfalls zwei getrennte *b*-Zacken besitzt, die gewöhnlich verschiedenen Erregungen in Zapfen und Stäbchen zugeschrieben werden. Diese Erklärung kann für die beiden *b*-Zacken des Boden-Eichhörnchens nicht richtig sein, da hier nur Zapfen vorhanden sind. Offensichtlich kann ein doppeltes *b*-System, das sich in mancher Hinsicht wie das Stäbchen–Zapfen-System der menschlichen Retina verhält, auch in einer Netzhaut mit einem einzigen morphologischen Rezeptortyp auftreten.

[1] Aided by a grant from the Division of Research Grants and Fellowships, National Institutes of Health, U.S. Public Health Service, and by a grant from the University Board of Research. Analysis of the data and writing of this report were carried out while the author was on sabbatical leave from the University of California and during the tenure of a Senior Postdoctoral Fellowship of the National Science Foundation. The author wishes to thank Sir Stewart Duke-Elder and Dr. H. J. A. Dartnall of the Institute of Ophthalmology, London, for making available the facilities of the Institute. It is a pleasure to acknowledge the help received from Dr. K. Tansley in many conversations about ground squirrels.

INTRODUCTION

MULTIPLE components have often been noted in the *b*-wave of the electroretinogram (ERG). CHAFFEE, BOVIE and HAMPSON (1923) called attention to these in the frog ERG and discussed the possibility that the first two of these (b_1 and b_2) were independent of each other and were associated with activity in cones and rods, respectively. Later publications by this group (MESERVEY and CHAFFEE, 1927; CHAFFEE and HAMPSON, 1924) reiterated this view and showed that these two components changed at different rates in response to decreasing the light intensity. The b_2-wave, initially the smaller of the two, became, relatively, the larger when the light intensity was decreased sufficiently. GRANIT and MUNSTERHJELM (1937) admitted that the multiple humps in the frog ERG could be of retinal origin and noted, especially at low stimulating levels, two *b*-waves which were thought to be related to retinal elements with different functional properties. ADRIAN (1944, 1945) was first to publish comprehensive and specific experimental evidence to support the hypothesis of a photopic–scotopic duality for the ERG. The dark-adapted human eye yielded an ERG consisting of an initial and rapid diphasic component and a second positive, slower elevation. The initial potential was evoked by flashes of red light whereas the slower wave was present in response to blue light. In addition, the slower component was absent in records obtained from the light-adapted eye. From all this as well as from other evidence Adrian concluded that the fast and slow *b*-waves were associated with cone and rod activity, respectively. Adrian extended his thesis to include the ERG of other vertebrates (1946). He concluded that animals, like the monkey and pigeon, which have mixed retinae with a relatively large number of cones, gave an ERG, like that of the human, with dual *b*-waves. From animals with a preponderance of rods (cat, rabbit, guinea-pig) Adrian obtained records without the typical fast wave. While adding certain modifications in specific interpretation, recent investigators (ARMINGTON, 1952, 1959; ARMINGTON and THIEDE, 1954; SCHUBERT and BORNSCHEIN, 1952; GOODMAN and ISER, 1956; RIGGS, 1958) of the human ERG have preserved the essentials of Adrian's proposal. The situation in respect to this proposal is less clear for the ERG of other vertebrates. Multiple *b*-waves were noted, for example, in the ERG of the horned toad (MESERVEY and CHAFFEE, 1927) even though the retina of this lizard was considered to be of the pure cone type. MESERVEY and CHAFFEE (1927) noted no differences in records from the "rod" portion and the "cone" portion of the alligator retina under experimental conditions where stray light was probably not significant in determining the responses. The mixed frog retina was found to give double-humped *b*-waves to all colors with no evidence of a wavelength specificity (CHAFFEE and HAMPSON, 1924). The turtle eye reacted to light with an ERG which showed both an initial fast wave and a second slower potential (DEANE, ENROTH-CUGELL, GONGAWARE, NEYLAND and FORBES, 1958). Yet both these components were reported to have similar spectral sensitivities. As the evidence stands no simple application of the duality hypothesis can generalize these data.

An approach not employed by Adrian is to select for study a mammal with a pure cone type of retina. Such mammals are rare but among them are certain genera of the squirrels, especially the ground squirrels (genus *Citellus*). Ground squirrels are know to have retinae with all the visual cells of the cone type (KARLI, 1951; VILTER, 1954; ARDEN and TANSLEY, 1955). No Purkinjé shift was detected (ARDEN and TANSLEY, 1955) and the ERG was of the type usually associated with the activity in cone systems (BORNSCHEIN, 1954; ARDEN and TANSLEY, 1955; TANSLEY, 1957). In addition, the threshold for the ERG and the curve of fusion frequency as a function of light intensity both indicated the absence of functional

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rods (BORNSCHEIN and SZEGVÁRI, 1958). Along with all this are the facts that the lenses of the ground squirrel eyes are quite yellow and the animals are strictly diurnal in habit of life. The total evidence suggests the visual system to be of the photopic type. Several years ago a study was begun of the eye of the antelope ground squirrel (*Citellus leucurus leucurus*). Some preliminary observations have already been published (CRESCITELLI and GARDNER, 1956; JOHNSTON and GARDNER, 1959). This paper is concerned with a description of the ERG of this rodent obtained in response to single and multiple flashes of white and colored light. The description is oriented toward the problem of the duality hypothesis as applied to the ERG of this animal.

METHODS

The animals, captured by means of live traps, were kept in the laboratory until ready for use. This rodent remained healthy and active in captivity and even succeeded in a few cases in rearing young. In preparation for an experiment a squirrel was allowed to enter a small dark chamber. He (or she) was then quieted by means of ether following which nembutal was injected intraperitoneally. The anesthetized animal was next secured to a head holder[2] made specially for this species. The squirrel was held by means of ear plugs and an adjustable upper jaw clamp. The body was allowed to lie free on a platform warmed to 40°C by means of hot water. The lids of the right eye were cut and retracted, the pupil was dilated by instillation of 1% atropine–epinephrine and a plastic contact "glass" made specially for this species was placed over the cornea.[3] The electrodes were cotton wicks attached to chlorided silver wires mounted inside of fine glass tubes which were filled with Ringer's solution. The external surface of the tubes was painted black to prevent the generation of photoelectric artifacts. The active electrode was in contact with the cornea of the right eye at the edge of the contact "glass". The second electrode made contact with the sclera at the posterior half of the right eye. This location of electrodes was chosen since it best prevented recording of the electrocardiogram which was a problem in these small animals. Control experiments in which one electrode was placed on the sclera of the posterior half of the right eye and the second electrode elsewhere on the head gave no indication that massed optic nerve discharges were led off by the scleral electrode. The animal was grounded by means of a needle inserted into the muscles of the left leg.

The ERG was recorded by means of two different systems. One involved a resistance–capacitance amplifier and a Grass ink-recorder (time constant of 400 msec); the other was by means of direct-coupled amplifier and cathode ray oscillograph (Dumont). Since the ground squirrel ERG has no very slow and no very fast components (Fig. 1) the more convenient ink-recording system was employed routinely to secure data. The oscillographic system was used to confirm and to check precision of recording by the former method. The oscillographic system made use of an electronic switch (Dumont) to divide the beam into two and so to display, precisely and simultaneously, the ERG and the stimulus signal. Photographs were made of single sweeps of the cathode ray beam, synchronized triggering being accomplished by means of a microswitch mounted on the shaft of the motor which operated the shutter.

The optical system is described only briefly since it is one which is conventional for this type of investigation. The light source was a single ribbon filament lamp (6 V, 18 A, d.c.)

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[2] I express my thanks to Mr. Aaron Klain of the Department of Zoology for the construction of this useful head holder. Much time and skill went into the making of this machine.

[3] Dr. Henry A. Knoll kindly made the measurements of corneal curvature needed to manufacture these "glasses".

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powered from an electronically regulated power supply (Nobatron). The light was collimated and then brought to a focus at the plane of the shutter. The latter consisted of a metal disc with sector cut out which rotated at constant speed. A piece of plane glass mounted behind the rotating disc reflected a small amount of light on to a phototube whose output served as a stimulus signal marker either for the second channel of the Grass recorder or for the electronic switch-oscillograph system. The light was collected and brought to focus at the plane of the pupil so as to present a Maxwellian view to the eye. The angle subtended at the eye was 25°, deliberately large so as to illuminate a large portion of the retina and so to minimize the effects of scattered radiation which are believed by some investigators (BOYNTON and RIGGS, 1951) to play a role in generating the ERG. The light was passed through 3 cm of water and in most of the experiments an additional infrared absorbing filter (Corning Aklo) was employed. By means of a thermopile, and using a filter which transmitted heat but no visible light, it was possible to show that the combination of water and Aklo filter removed all the longer radiations so that measurements made with the thermopile were true measures of the visible light. The thermopile output was read conveniently and quickly by use of an amplifier (Leeds and Northrop) and a dual range (0–10, 0–50 mV) recorder (Brown). The linearity of this light-calibrating system was checked by measurements of light intensities which were varied by means of calibrated neutral filters. In some experiments with colored light it was necessary to increase the intensity further in order to obtain large enough responses. To accomplish this the Aklo filter was removed but the thermopile could then not be employed since some infrared radiations were present. In such cases a photocell (Photronic) calibrated with respect to wavelength sensitivity was used to measure the light energy. The response of this cell at 700 mμ was 3 per cent of its maximum at 562 mμ. The measurements were therefore not significantly influenced by the longer radiations present when the Aklo filter was out of use, so that the output of the cell, read by means of a precision d.c. microammeter (Weston), was a true measure of the visible light. In these experiments with colored light when the Aklo filter was not in use, controls using a light-absorbing filter showed that the small amount of longer radiation striking the ground squirrel eye was without effect in generating a potential.

To vary the light intensity neutral density filters were inserted in the light path at a point just beyond the shutter. These filters were calibrated for transmission of different colors in the position in which they were used. The thermopile-recorder or Photronic microammeter was used in this calibration except for those neutral filters having density values of 2·0 and higher. In such cases a more sensitive photomultiplier system (Eldorado Electronics) was utilized. The neutral filters were not strictly neutral since the curves of density plotted against wavelength were systematically higher in the blue region. The density values which were actually used in this report were corrected values which account for this selective absorption. The intensity of the white light at the eye without neutral filter but with both water and Aklo filter in place, was, for the area of pupil illuminated, 275 ft-c. (new candles). This figure was obtained through use of a Weston illumination meter in the same position as the eye. To obtain colored illumination Farrand interference filters were placed in the collimated portion of the light path. These filters have half-band widths of 11 to 20 mμ and transmissions of 23 to 33 per cent. The spectral transmissions of these filters were checked with a recording (Hardy) spectrophotometer. The energy of the colored light was determined, as already indicated, with a thermopile-recorder when the Aklo filter was in place or with the Photronic microammeter when this filter was out. The Aklo filter, when in use, reduced the light energy by a factor of 2 to 4 depending on wavelength.

It is clear that the type of shutter used in this work did not produce stimulus wave forms which rose and fell rapidly. Oscillographic records of the light stimulus made by placing a phototube in the position of the eye showed that at the shutter disc speed which was normally employed the rise and decay time of the light was about 10 msec. The stimulus durations given in this report are values measured between the midpoints of the rise and decay portions of the stimulus wave.

To analyze the data it was necessary to measure certain features of the records. These measurements were made by several techniques. The cathode ray oscillograms, photographed on 35 mm film, were projected and measurements were taken from the enlarged projections. The ink on paper responses were either first photographed on 35 mm film and then projected or, more commonly, the records were measured directly by means of a device made by Mr. A. H. Church of the Institute of Ophthalmology. This instrument permitted the records, illuminated from below, to be measured through the use of two independently adjustable metal straight edges. The two edges were set to span the feature of the records which were to be measured, the distance between the edges being read off a 25 mm full travel dial gauge which was driven by one of the edges. Readings which were reproducible to 0·05 mm were quickly and comfortably made with this device.

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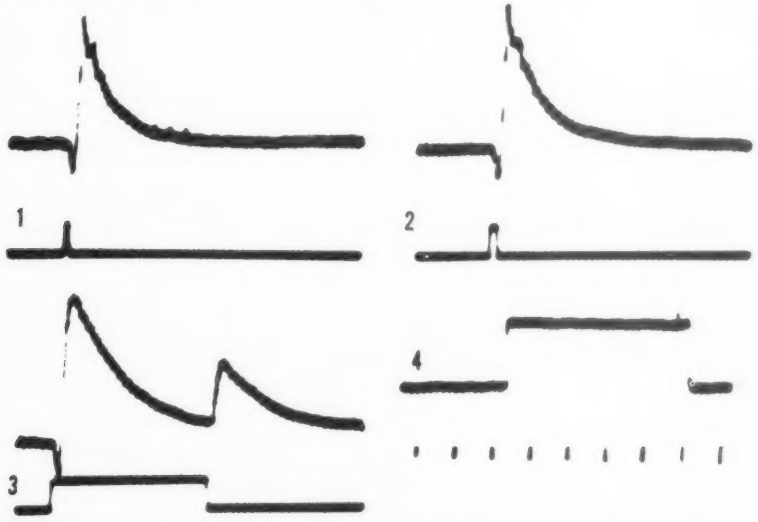

FIG. 1. Electroretinograms obtained with d.c. amplifier-cathode ray oscillograph from dark-adapted eye. Stimuli were brief flashes (9 and 18 msec) and a long flash (420 msec) of white light (275 ft-c.). Stimulus signals below each response. Calibrating voltage of 500 μV (record 4) and time lines 100 msec apart.

RESULTS

1. *General Description*

Representative records made with the direct-coupled amplifier and cathode ray oscillograph (Fig. 1) illustrate the following features of the ground squirrel ERG. There was a prominent *a*-wave with a peak which was reached in 20 to 27 msec after the start of the stimulus. In response to stimuli of longer duration (record 3) the *b*-wave was smoothly peaked. Brief light flashes often elicited *b*-waves with multiple humps (records 1 and 2) of which two (the b_1- and b_2-waves) were the most prominent. The b_1-wave reached a peak in

about 50 to 65 msec after the start of the stimulus and the corresponding time for the b_2-wave was 60 to 80 msec. The *b*-wave declined smoothly without showing any evidence of an added elevation such as the *c*-wave. An off-effect or *d*-wave appeared if the stimulus duration was sufficiently long (record 3). The *d*-wave increased in magnitude and a longer time was required to reach its peak as the stimulus duration was increased. Two or more components sometimes appeared to make up the off-effect. The ERG of this ground squirrel is of the type usually associated with activity in cone systems.

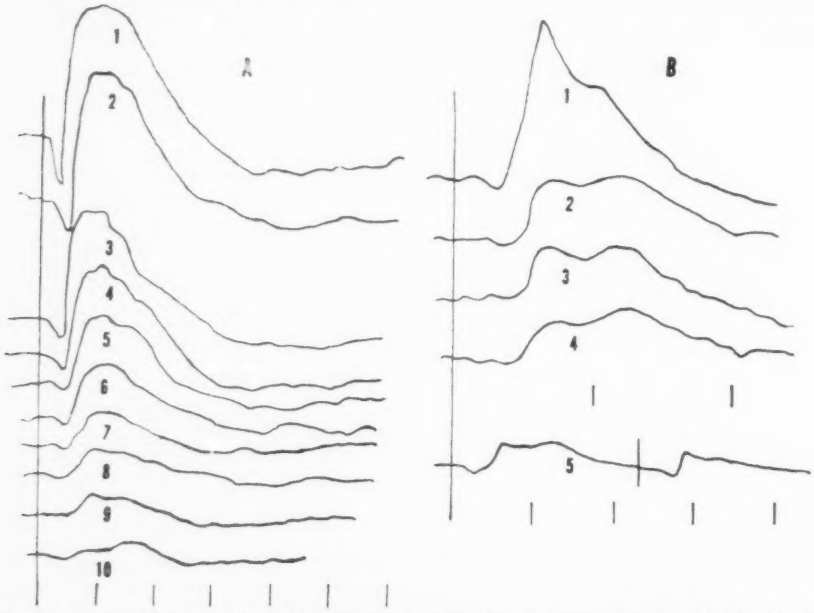

FIG. 2(A). Response to a brief flash (18 msec) of white light at intensities of 275, 95, 29, 10, 2·8, 0·83, 0·28, 0·14, 0·08 and 0·03 ft-c. (records 1–10). Eye was dark-adapted.

FIG. 2(B). Responses to a brief flash (18 msec) of white light at 275, 95, 64 and 29 ft-c. (records 1–4). Record 5: responses to two 18 msec flashes of white light (3 ft-c.) at interval of 235 msec. Time lines indicate 100 msec.

2. *Evidence for Functionally Different Components in the* b-*wave*

(*a*) *Effect of varying stimulus magnitude.* It was suggested by the records in Fig. 1 that the *b*-wave elicited by brief light flashes was compound and that among its components were included an initial, more sharply peaked wave (b_1) and a second, more roundly shaped elevation (b_2). These two were not always evident in records obtained in response to flashes at higher intensities. They could be brought out by decreasing the stimulus strength. With this procedure it was shown that the b_1-wave decreased at a greater rate as stimulus intensity was lowered and that the b_2-wave had a lower threshold, making it possible to isolate the b_2-wave by lowering the light intensity. This behaviour is illustrated in Fig. 2. The records in column A illustrate the point that a *b*-wave showing no evidence of duality (record 1) could be resolved into two components of which the second, at first the smaller of the two (record 9), eventually became the larger (record 10) as stimulus intensity was reduced. The top four records in column B also show the two *b*-waves and the faster decline of the initial component. The results of a complete experiment which illustrates the course of change of the two *b*-waves as stimulus intensity was lowered are given in Table 1 (flash-1).

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TABLE 1. MAGNITUDES (IN μV) OF THE TWO *b*-WAVES AS A FUNCTION OF (a) WHITE LIGHT INTENSITY AND (b) CONDITIONING. TWO BRIEF FLASHES (18 msec) OCCURRING 208 msec APART

Light intensity (ft-c.)	b_1-wave (μV)		Change (%)	b_2-wave (μV)		Change (%)
	Flash-1	Flash-2		Flash-1	Flash-2	
275	366	344	6·0	322	244	24·2
221	366	333	9·0	322	244	24·2
180	366	366	0	333	255	23·4
143	344	311	9·6	300	222	26·0
95	289	233	19·4	244	167	31·6
64	255	211	17·3	222	144	35·1
52	211	167	20·9	189	122	35·4
34	178	144	19·1	167	111	33·5
23	155	122	21·3	144	89	38·2
15	122	100	18·0	111	78	29·7
6·6	72	67	6·9	78	56	28·2
3·4	50	44	12·0	56	33	41·1
1·4	33	33	0	39	22	43·6

The *b*-waves were measured from the peaks of the *a*-waves.

The above statements refer to responses obtained to flashes of white light. They apply equally well to potentials following stimulation by flashes of colored light. In other words there appeared to be no wavelength specificity as far as the presence or behavior of these two components was concerned. This statement is supported by the electrograms of Fig. 3 in which are listed the responses to flashes at 454 mμ (records 1–8), 522 mμ (records 9–14), 606 mμ (records 15–19) and 631 mμ (records 20–26). With all these colors a reduction in light intensity resolved the *b*-wave into an initial, faster part and a second, slower potential. The latter had a lower threshold in all cases.

(*b*) *Effect of conditioning by light.* The two *b*-waves were also differentiated in respect to their selective behavior to light. This difference was readily demonstrated by use of repetitive flashes of light at an intensity which was low enough to resolve the *b*-wave into its two most prominent portions. The effect, which is invariably recorded, is illustrated in record 5 of Fig. 2B which gives the responses to two flashes 235 msec apart. The first response shows both waves of almost equal amplitude. The second response depicts the selective decrease of the second *b*-component. This action occurred not only to white light but also to flashes of color from 454 mμ to 631 mμ. The major portion of the conditioning occurred after only one flash and further repetition of the flashes caused only little further change. For example, in one experiment with twenty flashes at 2·5 per second the second response differed from the first as shown in record 5 of Fig. 2B. In contrast, the twentieth response differed from the second only in a minor way. An additional fact is that the percentage change of the *b*-components in two flash experiments was no less at low than at high stimulus intensities (Table 1). The results are suggestive of neurological rather than of photochemical adaptation.

Recovery from this conditioning was so rapid that flashes occurring at a frequency of one every two seconds produced responses which were much the same. An indication of the manner of this recovery is suggested by the superimposed tracings of Fig. 4. This figure summarizes the effect of a long (420 msec) conditioning flash on the responses to brief test flashes following at four different intervals after the conditioning flash. The unconditioned response, that is the response to the test flash not preceded by the long flash, is in all four

diagrams shown numbered 1 (dotted). When the interval between conditioning and test flashes was 83 msec (record 2) both *b*-components were reduced but the second one much more so. At an interval of 130 msec (record 3) the b_1-wave showed considerable recovery but the second wave was still largely depressed. This record also points to the fact that the b_1-potential isolated in this way was a relatively fast component having a duration, measured from the peak of the *a*-wave, of about 35 msec. At a flash interval of 230 msec (record 4) the first potential was back to normal while the later component was in the early phase of its recovery. The final diagram (record 5) taken at a flash interval of 425 msec shows the b_2-wave well on its way toward recovery but still below normal.

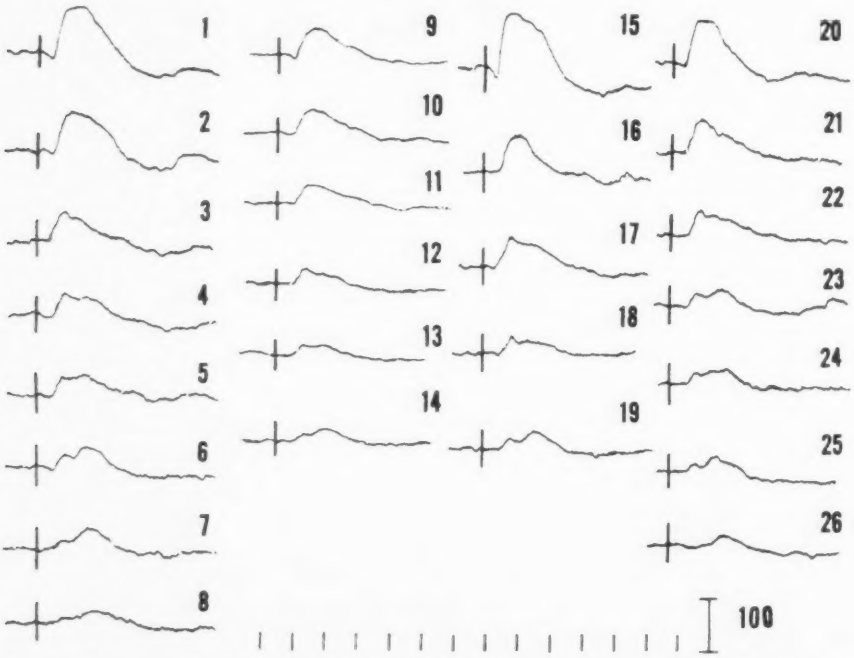

FIG. 3. Responses of a dark-adapted eye to brief flashes (18 msec) of colored light at various intensities. The colors were at 454 mμ (1–8), 522 mμ (9–14), 606 mμ (15–19) and 631 mμ (20–26). Relative intensities, measured by a thermopile and corrected for absorption by the crystalline lens, were: 454 mμ, 115, 32·2, 20·7, 10·4, 7·0, 4·0, 2·5, 1·6 (1–8); 522 mμ, 54·7, 36·5, 18·2, 15·8, 6·1, 2·0 (9–14); 606 mμ, 2591, 233, 72, 25·7, 12·4 (15–19); 631 mμ, 2094, 398, 189, 90, 56·6, 35·6, 18·9 (20–26). Note the relatively high sensitivity at 454 mμ. Time lines indicate 100 msec and calibration is 100 μV.

The effects of light adaptation were also examined by exposing the eye to the bright light (275 ft-c.) for periods of 5 or 10 min, after which the course of recovery was followed by means of brief test flashes delivered at intervals to the eye. In such experiments recovery of the *b*-components was slower than in the procedures just described in which conditioning to flashes of light was employed. In one experiment, selected because the b_1- and b_2-waves were clearly distinguished, light adaptation for 5 min depressed the b_1-elevation to 54 per cent of its dark-adapted level and the b_2-component to 39 per cent of its level, both these values being for a point 600 msec after shutting off the adapting light. Except for the first second of dark adaptation, during which the second component grew faster, the course of recovery of

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these two was much the same with a return to 80 per cent of the dark-adapted level in about 4·5 sec. The main point of this result is that recovery of both *b*-components was rapid and about the same, a result which is unlike the findings with the human ERG in which distinctly different rates of recovery were noted for the photopic and scotopic components of the *b*-wave (ADRIAN, 1945; JOHNSON, 1949; AUERBACH and BURIAN, 1955).

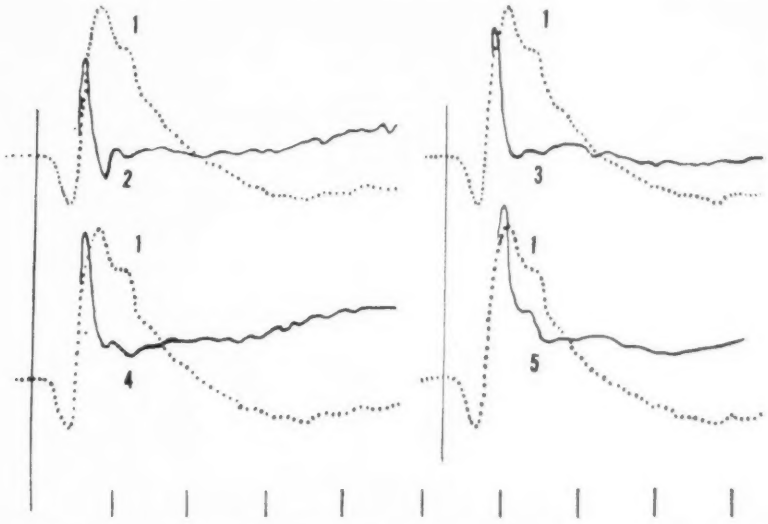

FIG. 4. The influence of a conditioning long flash (420 msec) on the responses to a brief (18 msec) flash falling at various intervals (given in text) after the long exposure. White light at 275 ft-c. The response to the brief flash alone is depicted by the dotted curves and numbered 1. Conditioned responses (2, 3, 4, 5) were superimposed by matching the peaks of the *a*-waves. Tracings were made of projections.

3. *Behavior of Other Components*

(*a*) *The* a-*wave*. The *a*-wave reacted to a conditioning flash by showing a cycle of change such as that illustrated in Fig. 5, in which are the results of stimulating the eye with two brief flashes with varying intervals between the two stimuli. When the flash interval was 20 msec (record 2) the response resembled that of a single exposure (record 1) and no second components attributable to the second flash were recorded. At an interval of 45 msec (record 3) there appeared a very small downward (negative) deflection indicating the first appearance of an *a*-wave to the second stimulus. For record 4, in which the separation was 70 msec, the second *a*-wave was well developed but still below the level of the unconditioned electroretinogram. At separations of 95 and 128 msec (records 5 and 6) the conditioned *a*-wave became hypersized following which it returned to normal (records 7, 8, 9, 10, 11). Graphs of *a*-wave amplitude (as percentage of the unconditioned amplitude) as a function of flash interval revealed the following phases in this cycle of change. From 0 to about 25 msec no *a*-wave was elicited by the second flash. From 25 to about 40 msec the *a*-wave appeared and developed although it was subnormal in size. From 40 to about 60 msec this component continued to grow reaching levels as high as 300 per cent. From 60 to about 200 msec the *a*-wave then decreased and returned to normal. An additional feature, especially well brought out in the experiment of Fig. 5, was that the oscillatory activity on the descending limb of the *b*-wave, which was present but not prominent in the electro-

retinogram to a single flash (record 1), was enhanced when the test flash fell at a critical interval after the conditioning flash. Record 5 obtained at 95 msec shows these oscillations especially well developed.

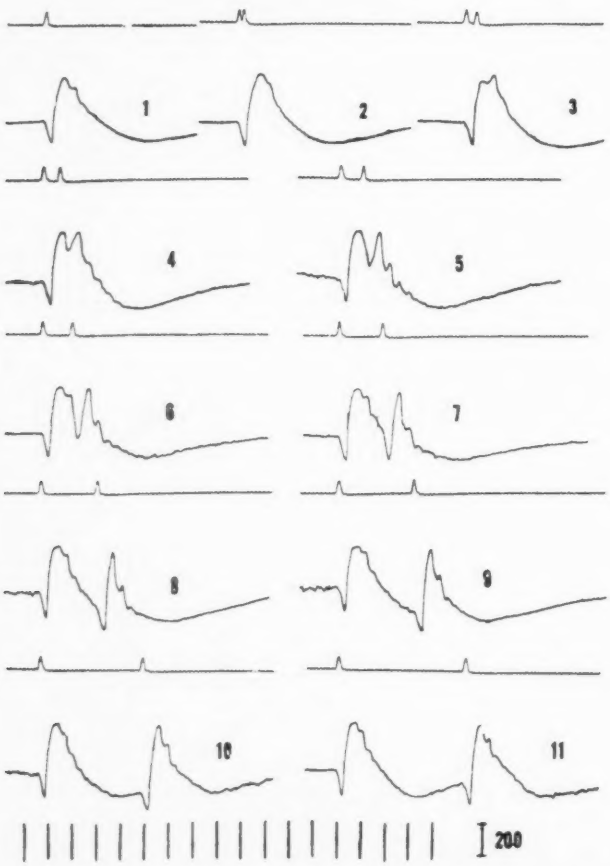

FIG. 5. The effect of two brief (18 msec) flashes of white light (275 ft-c.). Intervals between them were 20 msec (2), 45 msec (3), 70 msec (4), 95 msec (5), 128 msec (6), 183 msec (7), 233 msec (8), 313 msec (9), 425 msec (10), 530 msec (11). Upper markers are stimulus signals, time lines are 100 msec apart and calibration is 200 μV.

(*b*) *The* d-*wave*. In this section three characteristics of the ground squirrel off-effect will be briefly described. These are (a) the selective effect of bright light, (b) the *b*/*d* ratio in respect to stimulation by color and (c) the delaying effect of a light flash which fell during the early portion of the *d*-wave.

The first characteristic involved a selective reduction of the *d*-wave such as MESERVEY and CHAFFEE (1927) noted for the pure cone retina of the horned toad, during stimulation by very bright light. This action of bright light is made clear by tabulating the mean amplitudes of the *a*-, the *b*- and the *d*-waves elicited by a long flash of white light at 275 ft-c. and at an intensity about 2·5 times this value (Table 1). This increase in intensity was obtained simply by removing the infrared-absorbing filter. The same result was seen every time this

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filter was taken out, which was an increase in amplitude of the *a*- and *b*-waves but a simultaneous decrease in height of the off-effect, a clear selective action.

TABLE 2. SELECTIVE REDUCTION OF OFF-EFFECT BY INCREASING STIMULUS INTENSITY

Aklo filter	*a*-wave (μV)	*b*-wave (μV)	*d*-wave (μV)	N
In	48 (4·2)	213 (10·5)	57 (4·2)	7
Out	69 (4·8)	234 (9·6)	42 (3·0)	8
In	45 (3·0)	207 (9·6)	60 (3·9)	8
Out	63 (5·4)	228 (4·2)	39 (1·5)	8
In	42 (5·1)	204 (3·9)	54 (2·4)	7

Figures are means of N observations with standard deviations in brackets.

The second effect was the finding that electroretinograms in response to flashes of light at longer wavelengths tended to have greater off-effects. This was revealed by plotting the ratios of *b*- to *d*-wave magnitudes as a function of *b*-wave height, the *b*-wave amplitude being varied by altering the intensity of the stimulus flash. Over the experimentally feasible range of one log unit change in intensity the *b*/*d* values were not constant but rather changed systematically along a sigmoid curve. For flashes at 454, 469, 482, 501 and 522 mμ these ratios had a value of about 2·0 for all intensities from that which gave the largest (100 per cent) *b*-wave to intensities which elicited *b*-waves of 50 per cent height. From this point to *b*-waves of 25 per cent height the ratios rose rapidly to values above 3·0. For flashes at 560, 590 and 606 mμ the *b*/*d* ratios started similarly at about 2·0 but only rose to values of about 2·2. In other words in the lower range of intensity, responses with equal *b*-wave heights did not have, for the entire range of colors, equal *d*-waves. Instead, the flashes at longer wavelengths tended to have larger *d*-waves. The nature of the results is illustrated by the data in Table 3 in which the *b*/*d* ratios are listed for responses to flashes of different color, the responses being selected on the basis of approximately equal *b*-waves. No great emphasis need be placed on these results at present since it is doubtful whether a rigid statistical test would confirm the above conclusion. The difficulty was to obtain enough responses with

TABLE 3. EFFECT OF WAVELENGTH

Ratios of *b*- to *d*-waves in electroretinograms chosen for their approximately equal *b*-waves.

Wavelength (mμ)	Experiment 1		Experiment 2	
	b-wave (μV)	*b*/*d*	*b*-wave (μV)	*b*/*d*
454	161	4·2	238	3·5
469	155	4·8	212	3·1
482			200	3·0
501	167	4·3	216	3·2
522	177	3·2	219	3·1
560	161	2·9	200	2·7
590	138	2·9	187	2·3
606	158	2·6	209	2·2

d-waves of amplitude great enough to make a thorough study. Nevertheless it would be unwise to ignore these results for, as will be shown in another report, evidence was obtained which demonstrates the existence of a specific wavelength effect with respect to the on–off potentials evoked at the visual cortex of this ground squirrel. It is likely that this central effect has a peripheral basis. It is of some interest to note here the recent observation of GOLDSMITH (1960) that the off-effect from the compound eye of the worker honey-bee varies with wavelength, being greater at longer wavelengths.

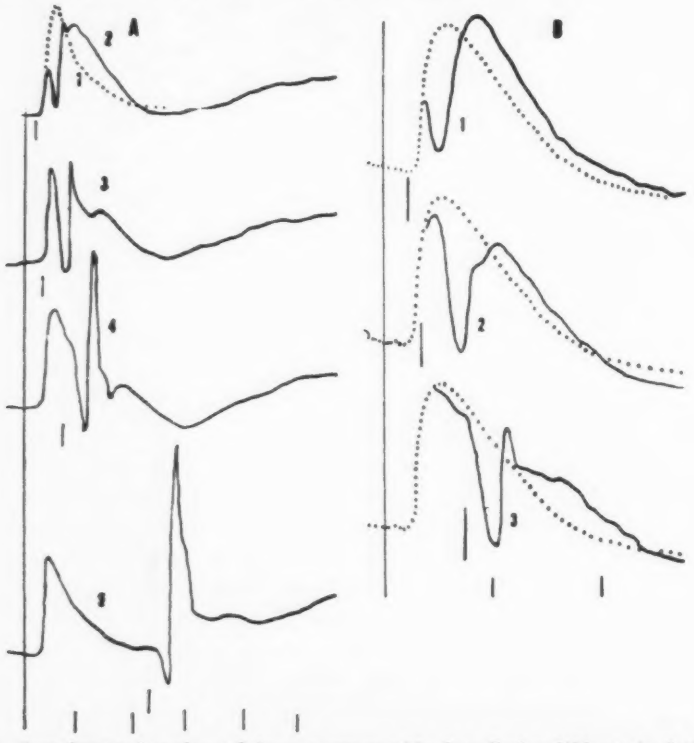

FIG. 6. Superimposed tracings of *d*-waves generated by long flashes (420 msec) of white light (275 ft-c.) and of responses to brief flashes (18 msec) at various intervals after the long flashes.
Column A: Record 1, *d*-wave alone (dotted) on which is superimposed (full line) the combination *d*-wave and response to brief flash which followed after 25 msec. Note the peaked *b*-wave followed by the delayed *d*-wave. Records 3, 4 and 5, combination *d*-wave and responses to brief flashes at intervals of 35, 75 and 240 msec.
Column B: *d*-wave alone (dotted). Records 1, 2 and 3, flash intervals were 25, 35 and 75 msec. Time lines indicate 100 msec. Tracings were made from projections.

The delaying effect of a flash is described in the superimposed tracings in Fig. 6B in which the dotted portion represents the course of a *d*-wave alone and the full portion shows the way this course was altered when a brief flash followed at three different intervals after the end of the long flash which generated the off-effect. When the brief stimulus occurred 25 msec after the long flash (record 1) the result was, in addition to the *a*-wave of the brief flash, a delay of the *d*-wave by about 30 msec. Otherwise the course of the off-effect was unaltered. This is indicated by the fact that the delayed and undelayed *d*-waves were superimposable along their entire course when their peaks were superimposed. That the

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delayed tracing was in fact the *d*-wave and not the *b*-wave of the brief flash is suggested by the tracings in Fig. 6A which show the *b*-wave to the brief stimulus as a separate and fast component not at all resembling the slower *d*-wave. GRANIT and RIDDELL (1934) recorded the same effects in a study of the frog eye. They noted not only the retardation of the *d*-wave through the influence of a light flash which fell early in the off-sequence but also the cycle of the *a*-wave and the sharpening of the *b*-wave as reported here (Figs. 4, 5, 6).

DISCUSSION

The ERG of the antelope ground squirrel proved to be of the type usually associated with activity in cone systems. There was no *c*-wave, the *d*-wave was prominent, light adaptation had a relatively small effect, except when examined under conditions in which the test flash intensity was 0·1 or less that of the adapting light, and recovery from such adaptation was rapid. The notable increase in magnitude of the *a*-wave which occurred 40–200 msec after a conditioning flash may also be associated with activity in cone systems. In agreement with BORNSCHEIN and SZEGVARI (1958) this behavior for the *a*-wave was not found by the author in the rod-dominated guinea-pig eye.

The special feature of the present results was the finding in this pure cone retina of multiple *b*-waves of which the two most prominent components showed behavior which in some respects was like that of the photopic and scotopic waves noted by ADRIAN (1944, 1945, 1946). This similarity involved the wave form as well as the behavior in relation to changes in stimulus intensity and to light adaptation, as explained in the previous section. These resemblances might lead one to suppose that this duplex system in the ground squirrel is basically analogous to the two *b*-waves of the human ERG. This, in turn, might lead to doubts (as in fact it has in the author's mind) about the duality hypothesis or else to questions about the pure photopic nature of the ground squirrel retina. This dilemma is avoided, for the present at least, by pointing out two clear differences between the double *b*-waves of the ground squirrel and the system in the human and monkey ERG. The first difference is that the b_2-wave of the ground squirrel ERG recovered rapidly (in 2–3 min) from light-adaptation, whereas dark adaptation in the human and monkey system was much slower. ADRIAN (1946), for example, found the second component in the monkey ERG to require an interval of 15–30 min in order to return to normal size after a period of light adaptation sufficiently long to completely suppress this wave. Similar slow recoveries of the human scotopic *b*-wave were reported to occur by ADRIAN (1944) and by AUERBACH and BURIAN (1955). The second difference was in relation to the responses to color. The ground squirrel ERG had both *b*-waves at all wavelengths from 454 to 631 mμ and there was no indication that when the amplitudes of the b_2-waves were equal for the responses to blue and to red light (Fig. 3), the magnitudes of the b_1-waves were markedly different. In contrast to this the responses from the human eye (ADRIAN, 1944, 1945) showed no evidence that they could be matched in this way. At intensities for which the second components were about equal in the case of flashes of blue and of orange-red light, for example, the response to the orange-red flash included a large initial fast wave which was absent in the case of the response to the blue light.

It may be concluded, therefore, that the b_2-wave in the ground squirrel ERG was the result neither of the activity in rod systems nor of cones with a spectral sensitivity markedly different from the cones involved in the b_1-component. Detailed knowledge concerning the extent and nature of summation in pure-cone retinae such as those of the ground squirrels is lacking but the work of KARLI (1951) has already demonstrated that in such retinae,

though the ratio of visual cells to ganglion cells is low, it is not the same over the entire retina. If it is assumed, therefore, that functional convergence is present then the b_1- and b_2-components may be interpreted as electrical signs of activity with different degrees of convergence. This was probably what TANSLEY (1957) had in mind when she discussed the change in form and latency of the *b*-wave in the squirrel ERG as stimulus intensity was lowered. It was also the suggestion of AUERBACH to DEANE, ENROTH-CUGELL, GONGAWARE, NEYLAND and FORBES (1958) to explain the dual components of the turtle ERG. The two *b*-waves of the ground squirrel ERG are probably of functional significance in vision. This thought is the outcome of another investigation, to be published shortly, in which it will be shown that two separate potentials functionally associated with the dual *b*-waves were recorded from the ground squirrel visual cortex in response to brief light flashes.

SUMMARY

1. The ERG of the antelope ground squirrel was examined in relation to the intensity, duration and color of the stimulating light as well as in relation to the effects of double and multiple flashes.

2. The ERG was of the type normally associated with activity in cone systems with well-developed *a*- and *d*-waves and with no *c*-wave.

3. The *b*-wave was multiple and two components (b_1- and b_2-) were most prominent. Of these two the b_2-system had the lower threshold and was more depressed by light adaptation although recovery from such adaptation was as rapid for the second wave as for the first.

4. There was no color specificity associated with these two systems and both were found in about the same ratio to each other at all wavelengths from 454 to 631 mμ.

5. The two *b*-components were similar to the photopic–scotopic system in the human ERG in respect to wave form and in relation to the behavior to light adaptation and to variations in light intensity. The ground squirrel and human *b*-waves did show differences with regard to the responses evoked by flashes of colored light and with regard to the speed of recovery from light adaptation. The two systems in these different mammals are not considered to be analogous.

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SPECTRAL SENSITIVITY CURVES OF DIURNAL SQUIRRELS

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Abstract—Spectral sensitivity curves were constructed for four species of ground squirrel, two species of tree squirrel and one species of chipmunk using the stimulus intensity required to produce a constant electroretinogram as the criterion. All these species have an apparently pure-cone retina although the retinal structure of the two tree squirrels differs somewhat from that of the ground squirrels and chipmunk. There was no evidence of a Purkinje shift. The spectral sensitivity curves of all seven species were very similar. The curves showed two maxima, one at about 535 mμ, the other at about 490 mμ. The relative heights of these maxima varied from one experiment to another but the factors responsible for this variation could not be determined. Adaptation to blue light depressed the maximum at 490 mμ while adaptation to green or orange light depressed that at 535 mμ. Evidence was obtained that the mechanisms responsible for the two maxima were to some extent antagonistic. The possible nature of these two mechanisms is discussed in the light of recent work on the photosensitive substances extractable from the retina of the common gray squirrel. There was some evidence for a further mechanism maximally sensitive between 450 and 460 mμ at least in some of the species investigated.

Résumé—On a déterminé les courbes de sensibilité spectrale pour quatre espèces d'écureuils terrestres, deux espèces d'écureuils arboricoles et une espèce de "chipmunk", en utilisant comme critérium une valeur constante de l'électrorétinogramme. Les rétines de toutes ces espèces ne possèdent apparemment que des cônes, bien que la structure rétinienne des deux espèces arboricoles diffère quelque peu de celle des espèces terrestres et du "chipmunk". Il n'y a pas trace d'effet Purkinje. Les courbes de sensibilité spectrale des sept espèces se ressemblent toutes beaucoup; elles présentent deux maximum, l'un vers 535 mμ, l'autre vers 490 mμ; les hauteurs relatives de ces maximum varient d'une expérience à l'autre, sans qu'on puisse déterminer les causes de ces variations. L'adaptation par la lumière bleue abaisse le maximum de 490 mμ tandis que l'adaptation par des lumières verte ou orange abaisse celui de 535 mμ. Il semblerait que les mécanismes responsables de ces deux maximum soient en quelque facon antagonistes. La nature possible de ces deux mécanismes est discutée à la lumière de travaux récents sur les pigments photosensibles que l'on extrait de la rétine de l'ecureuil gris commun. Dans certaines des espèces étudiées tout au moins, il pourrait exister un autre mécanisme dont le maximum de sensibilité se situerait entre 450 et 460 mμ.

Zusammenfassung—Die spektrale Empfindlichkeit wurde bei vier Exemplaren des Boden-Eichhörnchens, zwei Exemplaren des Baum-Eichhörnchens und einem gestreiften Eichhörnchen untersucht, indem die zur Erzeugung eines konstanten Elektroretinogramms notwendige Lichtintensität ermittelt wurde. Alle drei Arten besitzen augenscheinlich nur Zapfen in der Netzhaut, obwohl die Netzhautstruktur der beiden Baum-Eichhörnchen etwas von der der Boden Eichhörnchen und des gestreiften Eichhörnchens abweicht. Ein Purkinje-Effekt hat sich nicht gezeigt. Die spektralen Empfindlichkeitskurven waren bei allen sieben Exemplaren sehr ähnlich. Sie zeigten zwei Maxima, eines bei etwa 535 mμ, das andere bei etsa 490 mμ. Die relative Höhe der beiden Maxima änderte sich von einem Experiment zum andern; die Ursachen dieser Veränderung konnten nicht bestimmt werden. Adaptation an blaues Licht verkleinert das Maximum bei 490 mμ, während Adaptation an grünes oder oranges Licht dasjenige bei 535 mμ verkleinert. Es konnte gezeigt werden, dass die für die beiden Maxima verantwortlichen Mechanismen bis zu einem gewissen Grade antagonistisch waren. Die Mechanismen werden im Hinblick auf Untersuchungen diskutiert, die kürzlich an den aus der Netz-

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haut des gewöhnlichen grauen Eichhörnchens extrahierten lichtempfindlichen Stoffen durchgeführt wurden. Einige Hinweise auf einen weiteren Mechanismus, der zwischen 450 und 460 mμ am empfindlichsten ist, wurden mindestens in einigen der untersuchten Exemplare gefunden.

IN PREVIOUS investigations on the spectral sensitivity of two species of the squirrel family, the gray squirrel, *Sciurus carolinensis leucotis* and the souslik or European ground squirrel, *Citellus citellus*, one of us (ARDEN and TANSLEY, 1955a, b) recorded curves with their maxima around 530 mμ. In the case of the gray squirrel the curve was an unexpectedly narrow one reminiscent of one of GRANIT's modulator curves.[1] The mean souslik curve, on the other hand, was much broader on the short-wave side of the maximum reflecting a raised blue sensitivity which was not present in all experiments. It seemed possible that we were dealing with a second visual mechanism maximally sensitive to the shorter wavelengths and rather capricious in its manifestations. Again we could not be certain whether the different sensitivity curves we found reflected a true difference between the tree squirrels and the ground squirrels, so that it seemed desirable to repeat the experiments with other species, a more satisfactory method of recording the spectral sensitivity curves and a greater number of individual animals from each species.

MATERIALS AND METHODS

The experiments were done on four species of ground squirrel: *Citellus beecheyi* (four animals), *Citellus tridecemlineatus* (two animals), *Citellus variegatus buckleyi* (four animals) and *Citellus lateralis* (four animals); on two tree squirrel species, the gray, *Sciurus carolinensis leucotis* (four animals) and the American red, *Tamiosciurus hudsonicus loquax* (two animals); and on one chipmunk species, *Eutamias amoenus luteiventris* (two animals). Histological preparations were made of the eyes of all species with the exception of the gray squirrel which had already been examined (ARDEN and TANSLEY, 1955a).

The animal was removed from its cage in a nylon fish-net and given 20% urethane solution intraperitoneally, the usual dose being 2 g/kg body weight. After the animal was anaesthetized the eyes were treated with 0·5% proparacaine hydrochloride (Ophthaine) to produce topical anaesthesia of the cornea and with 10% phenylephrine (Neosynephrine) viscous to dilate the pupil.

The corneal electrode was incorporated in a specially made plastic contact glass and was a silver wire; the contact glass was filled with methyl cellulose saline. The indifferent electrode was a small silver plate (an EEG electrode disc) held in position on a shaved area of the forehead, which had previously been smeared with electrode jelly, by means of a rubber band round the upper jaw. Some of these electrodes were photosensitive and care was taken to shield them from the stimulating light. The animal was grounded by means of a bulldog clip wrapped in saline-soaked cotton wool attached to one ear.

The light stimulus was provided by a xenon arc and double interference filters as described by COPENHAVER and GUNKEL (1959). Three additional filters were used with maximum transmissions at 480, 509 and 545 mμ respectively. Neutral density filters were used to regulate the stimulus intensity as in Copenhaver and Gunkel's investigation. Most of the experiments were done with the light focused on the cornea so that it would be in Maxwellian view. In a few cases field sizes of 1° and 60° were also used. The intensity produced at the eye without neutral or color filters in the light beam was 7500 lux. The earliest experiments were done with the 32 per sec flickering stimulus used in human

[1] GRANIT (1947).

observations by Copenhaver and Gunkel, but this type of stimulus was found to be of no advantage and for most of the experiments a light flash of 1/4 sec duration was used. For observations taken during light adaptation the stimulus was presented once a second; in dark-adapted experiments the stimuli were not given oftener than once a minute.

For the color-adaptation experiments a special light source was contrived consisting of a standard 100 W Sylvania zirconium concentrated arc lamp provided with condensers and a filter holder. So that there should be no interference with the stimulating beam the adaptation light was concentrated and brought to the pupillary area of the contact glass by means of a curved Zeiss transilluminator tip of about 2 mm diameter. This tip in close proximity to the cornea acted like a point source and gave maximum illumination of the retina. Inconel neutral density filters (Bausch and Lomb) were used to vary the illumination when required. The color filters used were Eastman Kodak's Wratten 22 (orange), Wratten 58 (green), and Wratten 47 (blue). Their dominant wavelengths were 595, 534 and 480 mμ respectively.

The ordinary light-adapted experiments were done with the room lights on giving a level of 170 to 240 lux at the animal's eye.

In each experiment records of the response to each colored stimulus were taken starting with a check point at 531 mμ, then working through the spectral range usually starting at the red end, and finally checking back to 531 mμ at the end of the run. Runs were always made under both dark- and light-adapted conditions. In addition, in some experiments runs were made with an adapting color shining into the eye. For these the adapting light was used for 5 min before readings were begun and was kept on during the run, the spectral stimulus being superimposed on the adapting light. In the earlier experiments, the crystalline lens was removed from the experimental eye (usually the left eye) at the end of the experiment; it was then mounted in a special holder and its transmission at each stimulating wavelength measured by substituting a photocell for the eye. Then the lens and holder were removed and the measurements repeated using the interference filters alone. This procedure also provided a calibration for the xenon arc light source. In the later experiments the lens was extracted before recording began so that no correction for its spectral absorption was required. In all the species used for these experiments the lens is more or less yellow in color so that it was necessary either to correct for its transmission or to make the readings in its absence.

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Histology

When recording was complete, the upper part of the animal was intravitally fixed through the ascending aorta after washing out with isotonic saline. The fixative used was either Zenker's, Kolmer's, or Bouin's fluid. The control eyes were then removed and left overnight in the fixative. Embedding was in paraffin after removal of the lens and cornea and sections were cut at 6 μ; they were stained with haematoxylin and eosin, the azan mixture or by Feulgen's method.

RESULTS

Histology

The retinae of all seven species used in these experiments showed the general characteristics of a cone retina. Fig. 1 shows a section through the central area of the retina of the ground squirrel, *Citellus beecheyi*, showing a thin outer nuclear layer indicating a relatively small number of visual cells per unit area, with unusually thick inner nuclear and ganglion cell layers. It was found that the two species of tree squirrel, *Sciurus carolinensis leucotis* and

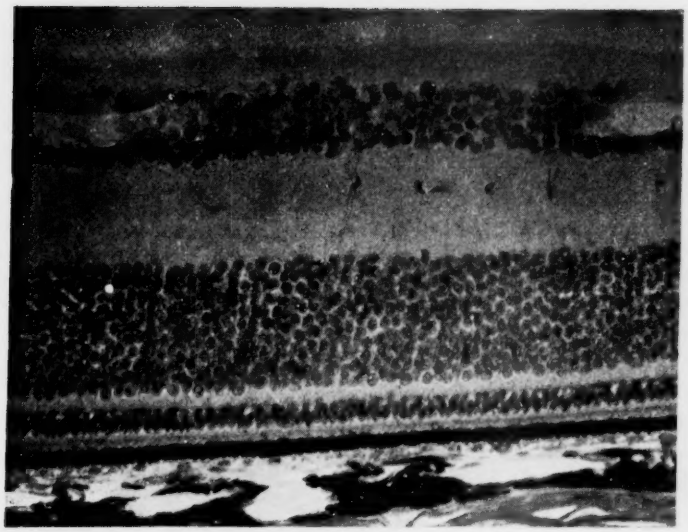

FIG. 1. The ground squirrel retina. Section through the central area of the retina of *Citellus beecheyi*. Note the exceptionally thick ganglion cell layer. Haematoxylin and eosin; Bouin. × 285.

The following numbering applies to Figs. 1, 2 and 3: 1, pigment epithelium; 2, cones; 3, outer nuclear layer; 4, outer fiber layer; 5, inner nuclear layer; 6, inner fiber layer; 7, ganglion cell layer; 8, optic nerve fiber layer.

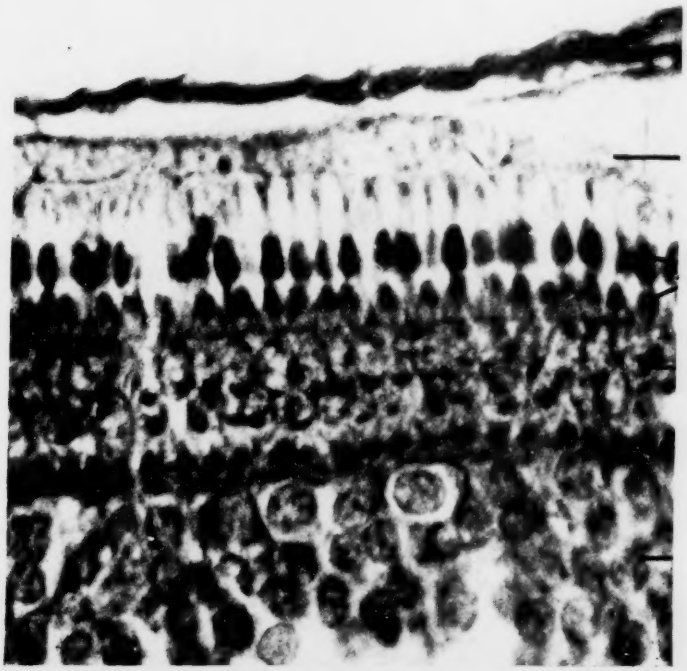

FIG. 2. The squirrel visual cells. Section through the outer retina of *Sciurus carolinensis leucotis*. Note the double layer of cones. Bleached; Azan: Kolmer. × 700.

[*facing p.* 156]

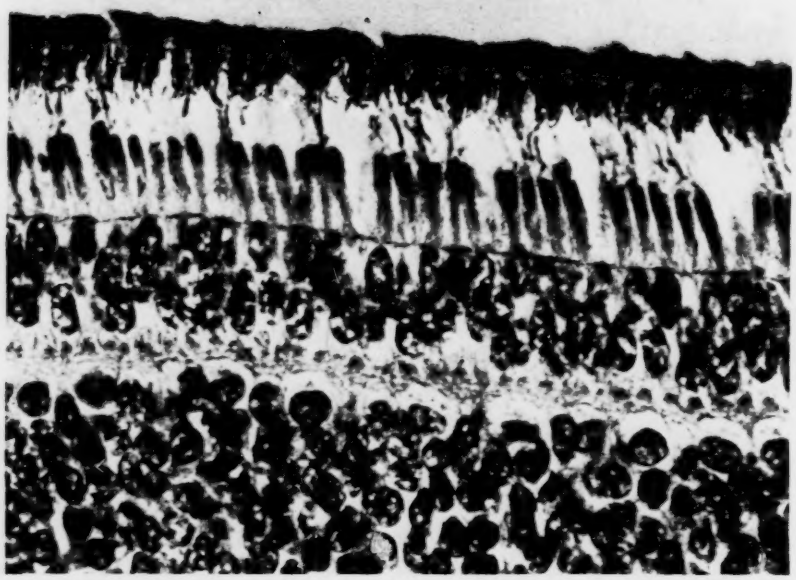

FIG. 3. The ground squirrel visual cells. Section through the outer retina of *Citellus lateralis*. Note the single layer of cones. Mallory's phosphotungstic acid haematoxylin; Zenker. ×775.

Tamiosciurus hudsonicus loquax, both had the double row of cones already described for *Sciurus carolinensis* (ARDEN and TANSLEY, 1955a). A high power view of the outer part of the retina of this species is shown in Fig. 2. The retina of another ground squirrel, *Citellus citellus*, has also been described by ARDEN and TANSLEY (1955b) and the four *Citellus* species used in the present investigation showed just the same picture, as also did the one chipmunk used, *Eutamias amoenus luteiventris*. A high power view of the outer retina of *Citellus lateralis* is shown in Fig. 3.

FIG. 4. The pure-cone electroretinogram. Two electroretinograms of *Citellus beecheyi* after removal of the lens. Dark-adapted; stimulus wavelength 531 mμ; no neutral filter; stimulus duration 1/4 sec.

Electrophysiological

Fig. 4 shows a pair of typical electroretinograms as recorded on the Grass encephalograph. These demonstrate the initial negative (downwards) *a*-wave, the second positive *b*-wave (upwards) and the striking positive off-effect. The negativity recorded after the *b*-wave is partly, but probably not wholly, an artifact due to the pen's overshooting. All eight channels of the encephalograph were used with a different amplification on each. It was found that excursions above about 10 mm were unreliable and those below 1 mm could not be read accurately. By using eight different amplifications, a much wider range of responses could be analysed. Most of the results analysed here are based on the amplitude of the *b*-wave (measured from the trough of the *a*-wave), but curves were also constructed for the responses of the *a*-wave and off-effect. It was found, however, that these did not

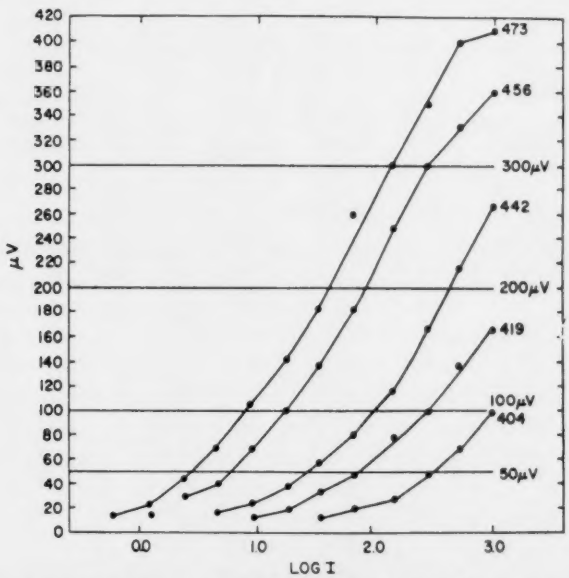

FIG. 5. Intensity-response curves. A group of representative intensity-response curves from a dark-adapted *Citellus beecheyi* after removal of the lens. Single flash 1/4 sec stimulus. Ordinates: amplitude of the *b*-wave in μV. Abscissae: log stimulus-intensity.

differ significantly from those obtained from the *b*-wave and they are not, therefore, considered separately.

The spectral sensitivity curves were calculated in the general way described by COPENHAVER and GUNKEL (1959). Intensity-response curves, mostly on *b*-wave amplitude, were plotted for each wavelength used in a run and the neutral filter density required to give a constant response determined. This density was corrected for differences in energy value for each spectral stimulus and for an equal quantum intensity spectrum; this correction included that for the crystalline lens in those experiments in which it was not extracted. A typical group of intensity-response curves from the short-wave part of the spectrum calculated for one run with the animal whose electroretinogram is given in Fig. 4 is shown in Fig. 5. Those from the rest of the spectrum were very similar. For this particular run criterion values of 300, 200, 100 and 50 μV were chosen for constructing the spectral sensitivity curves, but it

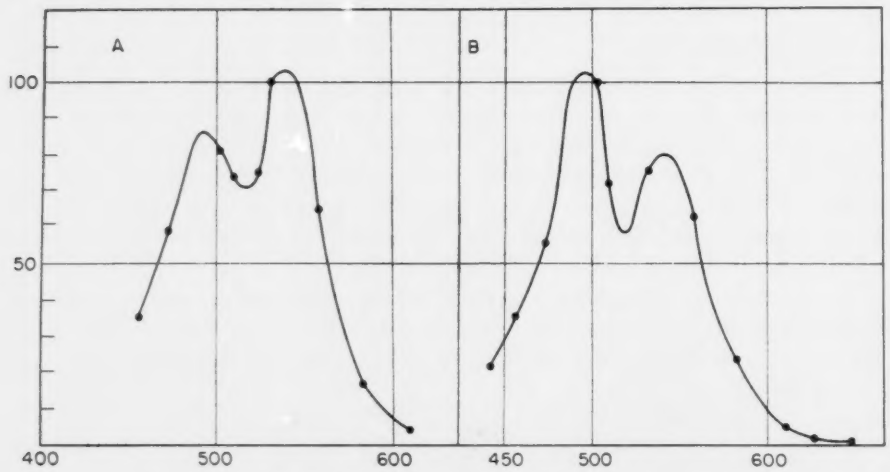

FIG. 6. Spectral sensitivity curves. Two spectral sensitivity curves from two different runs in one experiment on a dark-adapted *Citellus lateralis*. A. First run, 250 μV criterion. B. Second run, 100 μV criterion. Ordinates: percentage sensitivity. Abscissae: wavelength in mμ (equal quantum intensity spectrum).

was found that there was no significant difference between the curves for low and those for high criterion values (ARMINGTON, 1955). The density at each wavelength was then determined as a percentage of the density at the most effective wavelength and the points plotted against wavelength. To begin with, the curves were made by simply joining the individual points, but later, as a constant pattern emerged, the curves were drawn freehand.

No significant difference was found between the curves for the different species.

The curves were nearly all found to be double humped; occasionally the humps were nearly of the same height but more often one or other was markedly higher. Fig. 6 shows two typical curves, both from the same animal and taken under the same experimental conditions. None of our different experimental conditions was found regularly to produce one type of curve rather than the other. It was thought, for instance, that the "blue" hump might be due to scattered light. In order to test this point curves taken with a small (1°) field during dark adaptation, conditions which should favor stimulation of the retinal periphery by scattered light, were compared with ones taken with a large (50°) field in light adaptation, but there was no evidence that the former conditions favored the "blue" hump

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or that the latter favored the "green". Again it was considered possible that the presence of the yellow lens might protect a "blue" mechanism and so produce a higher relative sensitivity to the short wavelengths. It was for this reason that we originally removed the lens halfway through an experiment, repeating all the previous runs with an aphakic eye. Although the removal of the lens made it possible to get readings at shorter wavelengths than before, it had no effect on the relative sensitivities. No consistent difference was found between those curves taken during dark adaptation and those taken in light adaptation. There was therefore no evidence of a Purkinje shift in any of the species examined.

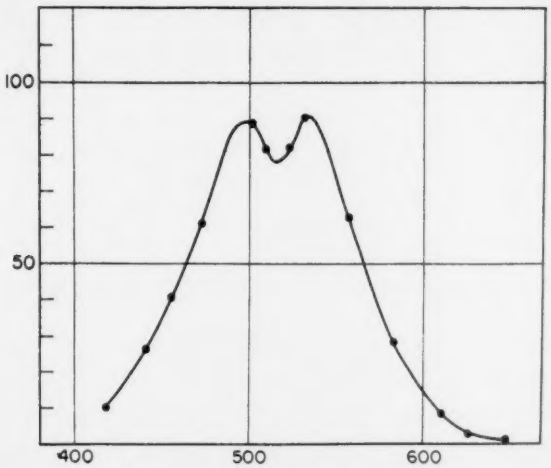

FIG. 7. Spectral sensitivity curve. Mean spectral sensitivity curve from all the experiments on *Citellus lateralis*. Ordinates: percentage sensitivity. Abscissae: wavelength in mμ (equal quantum intensity spectrum).

The two different types of curve illustrated in Fig. 6 were found in about equal numbers so that the mean spectral sensitivity curve for this species was nearly symmetrical with the two humps of about the same magnitude (Fig. 7). A fair proportion of the spectral sensitivity curves showed a distinct, albeit often very minor hump on the descending slope between 450 and 460 mμ (Fig. 11). When a mean curve for all the species investigated was drawn there was a distinct inflexion in this position which is outside the experimental error. The data for this mean curve (Fig. 8) are given in Table 1. It was calculated from the results of all the runs in which there was no evidence of a general change in sensitivity while the records were being made. It includes results in light- and dark-adaptation, with small, large and normal fields, using the amplitude of the *b*-wave, *a*-wave and off-effect, using high and low criterion values and for eyes with and without the crystalline lens. It was calculated from the records of 248 runs in all.

As a rule, our color-adaptation depressed the general sensitivity of the retina, but when the results were calculated as percentage of the maximum it was found that blue-adaptation depressed the hump at 490 to 500 mμ in all three experiments on *Citellus beecheyi*, in one out of two experiments on *Citellus lateralis*, in one experiment on *Citellus tridecemlineatus*, in one out of two experiments on *Citellus variegatus*, in one experiment on *Tamiosciurus hudsonicus* and in one experiment on *Eutamias amoenus*. Green- or orange-adaptation depressed the hump at 535 mμ in all three experiments on *Citellus beecheyi*, in two experiments on *Citellus tridecemlineatus*, in four experiments on *Citellus lateralis*, in two

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TABLE 1

Wavelength (mμ)	No. of readings	Mean sensitivity (%)	Standard error
648	46	2	0·4
626	97	3	0·3
610	199	9	0·1
583	247	29	0·7
558	248	62	0·9
545	32	81	1·0
531	248	86	0·9
523	248	85	0·9
509	143	83	1·0
502	248	88	0·9
480	32	67	2·0
473	246	60	0·8
456	229	46	0·9
442	113	28	1·0
419	24	12	2·0
404	8	7	1·0

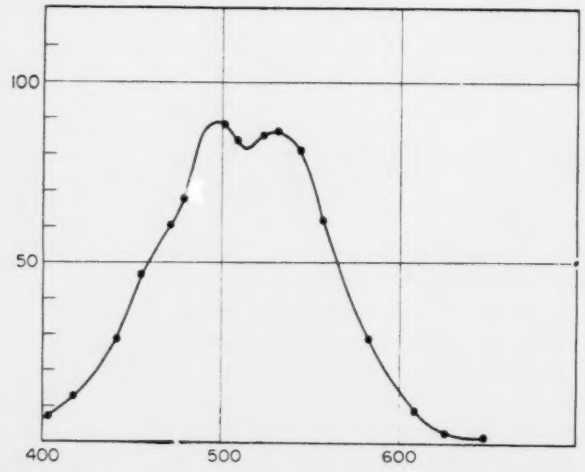

FIG. 8. Spectral sensitivity curve. Mean spectral sensitivity curve from all the runs on all seven species investigated. Ordinates: percentage sensitivity. Abscissae: wavelength in mμ (equal quantum intensity spectrum).

experiments on *Citellus variegatus* and in one experiment on *Tamiosciurus hudsonicus*, but had no effect in one experiment on *Eutamias amoenus*. The results of one of the experiments on *Citellus beecheyi* are shown in Fig. 9. In this figure the value at 531 mμ for the ordinary white-light-adapted sensitivity curve was taken as 100 per cent. For the curve taken with the blue-adapting light the value at 531 mμ was again taken as 100 per cent, while for the curve taken with the green-adapting light the value at 473 mμ was taken as 115 per cent, the figure for this point on the original white light-adapted curve; the values for the other wavelengths were calculated accordingly.

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The electrophysiological results were analysed for us by the Biometrics Branch of the National Institute of Neurological Diseases and Blindness. It was concluded (1) that our data for the seven species were homogeneous and could legitimately be combined, and (2) that our mean spectral sensitivity curve (Fig. 8) was a good description of the response data as a whole.

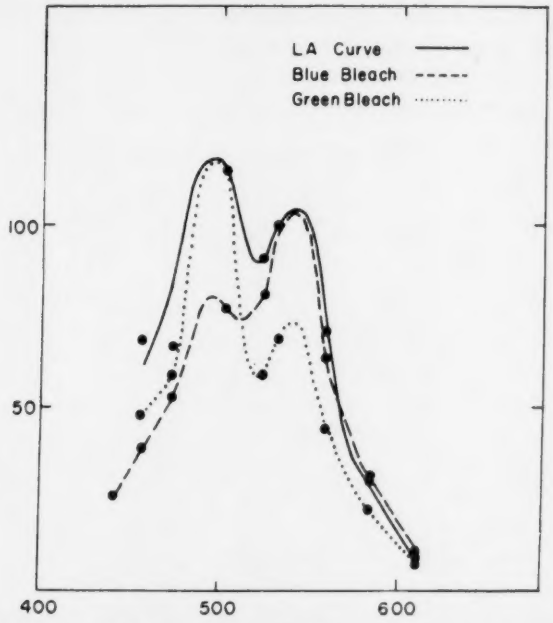

FIG. 9. The effect of color-adaptation. Three spectral sensitivity curves from one experiment on *Citellus beecheyi*. ——— light-adapted curve; - - - effect of blue-adaptation; ····· effect of green-adaptation. Ordinates: percentage sensitivity. Abscissae: wavelength in mμ (equal quantum intensity spectrum).

DISCUSSION

The histological examinations indicate that all *Citellus* species and at least the one chipmunk species used have a similar retinal structure with a single layer of cones, and that in the central retina there is probably a one-to-one relationship between these cones and the ganglion cells and, therefore, the optic nerve fibers. In the tree squirrels it seems likely that the cones always form a double layer and, since the ganglion cell layer is nowhere as thick in these species as it is in the central retina of the ground squirrel, it is improbable that there is a separate optic nerve fiber for each cone in any part of the retina. A similar retinal structure has been described by ROCHON-DUVIGNEAUD (1943) for the European red squirrel, *Sciurus vulgaris*. He recognized two groups of visual cells in this animal, but he used tangential sections and mistook the outer segments of the inner row of cones for rods. All the physiological evidence points to these being pure-cone retinae (TANSLEY, 1957).

The suggestion that a high blue sensitivity might be characteristic of the ground squirrels as opposed to the tree squirrels was not confirmed by the results of the present investigation where no significant difference was found between the sensitivity curves of the two groups. The shape of the spectral sensitivity curves came as a surprise. The long-wave part of the mean curve is in reasonable agreement with this part of the curves published by Arden and

Tansley for the gray squirrel and *Citellus citellus* and with that for the difference spectrum of the photolabile pigment found by WEALE (1955) in the living retina of the gray squirrel. However, the second peak at about 495 mμ was quite unexpected. It is true that a capricious high blue sensitivity was found by Arden and Tansley in *Citellus citellus* but their points in the relevant part of the spectrum between 480 and 545 mμ were too few and their standard error too great to make a satisfactory characterization of this part of the curve possible. Although Arden and Tansley did not suspect a second rise in sensitivity in their gray squirrels, if mean values are calculated for their published points there is some evidence for an inflexion on their curve at about 490 mμ although it is not very marked.

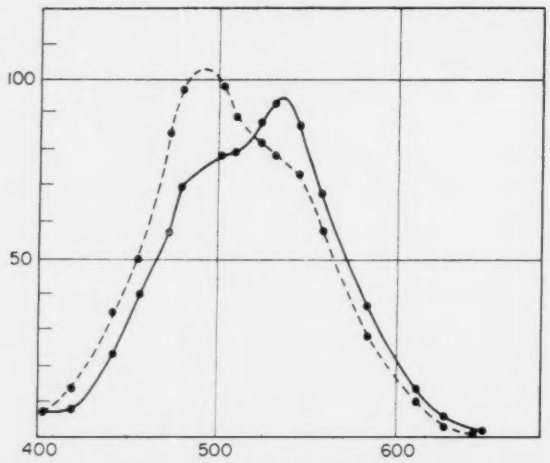

FIG. 10. Spectral sensitivity curves. Mean spectral sensitivity curves from all seven species. ——— mean curve from all the runs in which values at 523 and 531 mμ were high. – – – mean curve from all the runs in which values for wavelengths shorter than 523 mμ were high. Ordinates: percentage sensitivity. Abscissae: wavelength in mμ (equal quantum intensity spectrum).

We made many attempts to elucidate the nature of the mechanism responsible for the "blue" peak and were satisfied that it was not due to scattered light. It did not become more prominent in dark-adaptation nor if low criteria were used. The only way in which we were able to affect the shape of the curve in a predictable way was by using differently colored adapting lights while the records were being taken. Then we found that a blue-adapting light depressed the "blue" peak and a green- or orange-adapting light depressed the "green" one. This suggests that both peaks are rather closely associated with photosensitive mechanisms of different spectral sensitivities (Fig. 9).

Although the two peaks are of roughly the same height in the mean curve, the curves for individual experiments usually showed one or other to be the higher (Fig. 6) and this suggested that the two mechanisms might be in some sort of rivalry. In the hope of throwing some light on this idea all the curves were divided into two groups, one in which the values at 523 and 531 mμ were the highest and a second in which the highest values were found to be at wavelengths shorter than 523 mμ. When the means of these two groups were plotted separately the two curves shown in Fig. 10 were obtained. These show that when one peak is high the other does indeed tend to be very much reduced thus indicating some degree of rivalry between the mechanisms responsible for the two peaks.

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In trying to obtain more information about the mechanism responsible for the "blue" peak one must remember that the position of its maximum sensitivity is likely to be at a rather shorter wavelength than the 495 mμ shown in Fig. 8 or the 490 mμ shown in Fig. 10. Even the curve in Fig. 10 is probably pulled over somewhat towards longer wavelengths by the effect of the "green" mechanism and, in fact, if one plots the difference between the two curves in Fig. 10 for the shorter wavelengths the peak of the resultant curve falls at about 480 mμ. Recently DARTNALL (1960) has studied extracts of the gray squirrel retina and has found it to contain a rhodopsin with a maximum absorption at 502 mμ. This pigment on bleaching produced, in addition to the normal retinene, a photoproduct with its maximum absorption at 480 mμ. In considering the bearing of this result on the spectral sensitivity

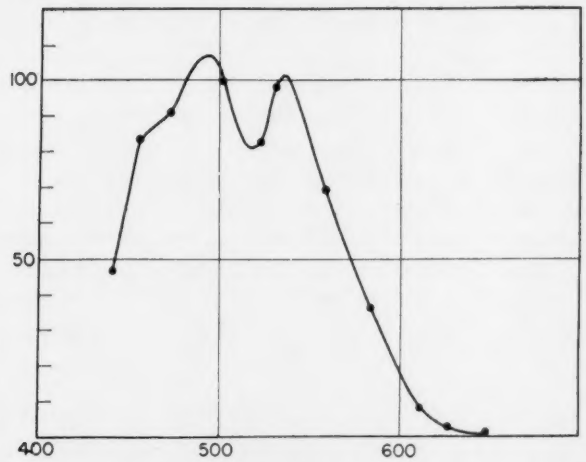

FIG. 11. Spectral sensitivity curve. Spectral sensitivity curve from a light-adapted *Citellus beecheyi* showing high values between 450 and 460 mμ. Ordinates: percentage sensitivity. Abscissae: wavelength in mμ (equal quantum intensity spectrum).

function found by Arden and Tansley and on the difference spectrum found by Weale in living squirrels Dartnall suggests that *in vivo* rhodopsin in the squirrel cones may bleach to a product having its maximum absorption at 480 mμ and which is itself photosensitive. He further suggests that the spectral sensitivity function with its maximum at around 530 mμ "may be mediated by a mechanism depending on the difference between the light absorbed by the rhodopsin at 502 mμ and that absorbed by the 480 photoproduct". He points out that if this is indeed the case a truly threshold sensitivity function would be expected to reproduce the 502 curve alone. None of our records was taken at this level since the electroretinogram is too insensitive a criterion to be useable at the absolute threshold. He also suggests that prolonged adaptation to long-wavelength light should result in a spectral sensitivity function which follows the form of the broad band 480 curve. The orange filter we used for adaptation had too broad a transmission band for adequate testing of this point. If sufficient adaptation was used entirely to eliminate the peak at 535 mμ the whole retinal sensitivity was so depressed that satisfactory records were unobtainable even in the short-wave part of the spectrum. In the light of Dartnall's findings a very tentative explanation of the spectral sensitivity curves found in this investigation might be that the 535 mμ peak is the result of interaction of some sort between two photosensitive substances with maxima at

502 and 480 mμ and that, in addition, the spectral sensitivity of the 480 pigment is responsible for the peak in this region. If, further, these pigments may be formed from one another, as Dartnall believes, this would explain the apparent rivalry of the mechanisms responsible, for our two peaks for the more of one pigment was present the less of the other.

In the mean curve of Fig. 8 there is a distinct inflexion around 450 to 460 mμ which, although small, is outside the experimental error. In 37 per cent of all the experiments in which records down to 442 mμ were obtainable the readings at 456 mμ were high, occasionally as high as or even higher than is shown in Fig. 11. In the remaining 63 per cent there was no evidence whatever of any special activity in this region. All but one of the curves with enhanced values at 456 mμ were obtained from light-adapted eyes. In the paper already quoted, Dartnall points out that interaction between possible activity mediated by the 480 pigment and that mediated by the 502 pigment might also give a spectral sensitivity function with a maximum at 448 mμ.

Spectral sensitivity curves obtained by electrophysiological methods with maxima or humps in the blue, usually capricious in their appearance, have often been reported in the literature. GRANIT (1947) in one of his figures shows a curve obtained from the guinea-pig retina by means of his microelectrode technique in which the maximum is at about 460 mμ with a secondary hump at about 535 mμ. DODT and ELENIUS (1956) working on single-fiber responses from the rabbit retina obtained some curves in which the maximum sensitivity is at 460 mμ. In two of these there is evidence of a secondary maximum near 500 mμ but in a third the secondary maximum is probably at a rather longer wavelength. ELENIUS (1958) shows two spectral sensitivity curves also from the rabbit obtained by means of the electroretinogram in which there was an enhanced sensitivity at 480 mμ. In both guinea-pig and rabbit the predominant visual pigment is, of course, rhodopsin. In this connexion it is worth mentioning INGVAR's (1959) paper on the cortex of the cat (also with a predominantly rhodopsin-containing retina) in which he suggests that there may be two scotopic mechanisms, one with maxima at about 460 and 530 mμ which is in rivalry with a second whose maximum is at 490 mμ. Ingvar found these mechanisms to be inherently unstable.

Although the mean curve of Fig. 8 shows no irregularity in the long-wave region of the spectrum, a comparison of this curve with Weale's for the gray squirrel does show a slight discrepancy at about 560 mμ which might indicate a further mechanism of some sort active in this spectral region, but the evidence is certainly not convincing enough to warrant drawing any conclusions on this point.

It has been argued that spectral sensitivity curves obtained by means of interference filters can show odd peaks which are really artefacts due to the special shape of the transmission bands of some filters of this type. This is not likely to be a complication in the present investigation since Copenhaver and Gunkel got perfectly smooth photopic sensitivity curves from human subjects with normal vision using the same apparatus and all but three of the filters we have used here. However, in order to test this point we did do two experiments on the dark-adapted rabbit and in these we obtained spectral sensitivity curves which satisfactorily fitted the rhodopsin absorption curve.

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SUMMARY

1. Using the electroretinogram as the criterion, spectral sensivity curves were obtained from seven different species of the squirrel family.

2. Histological examination showed that all these species have pure-cone retinae.

3. The curves showed two maxima at about 535 and 490 mμ respectively. There was evidence from color-adaptation experiments that the two maxima are associated with two mechanisms with different spectral sensitivities.

4. The possible nature of the mechanisms responsible for these two maxima is discussed.

5. There was some evidence for a further mechanism with its maximum activity between 450 and 460 mμ.

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ELECTRIC POTENTIALS OF RETINA AND CORTEX OF CATS EVOKED BY MONOCULAR AND BINOCULAR PHOTIC STIMULATION[1]

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Abstract—Electric potentials evoked by monocular and binocular photic stimuli were measured simultaneously at one position on the visual cortex of one hemisphere and at both retinae in anesthetized cats. Stimulation of the eye contralateral to the cortical electrode produced potentials with greater amplitudes and shorter latencies than the potentials evoked by stimulation of the ipsilateral eye. Potentials evoked by binocular stimulation were larger than those evoked by monocular stimulation, which represents an algebraic summation of the effects of activity conducted along crossed and uncrossed visual pathways. The *b*-wave response in the ERG was smaller in the binocular than in the monocular case, indicating mutual inhibition through centrifugal fibers. Monocular stimulation also gave ERG potentials in the unstimulated eye, though much lower in amplitude and reversed in polarity. These and other findings are discussed in relation to findings already in the literature.

Résumé—Sur des chats anesthésiés, on mesure les potentiels électriques que des stimuli lumineux monoculaires et binoculaires évoquent à la fois en un point du cortex visuel d'un hémisphère et dans les deux rétines. La stimulation de l'oeil contralatéral à l'électrode corticale produit des potentiels de plus grande amplitude et de plus courtes latences que les potentiels évoqués par stimulation de l'oeil ipsilatéral. Les potentiels évoqués par stimulation binoculaire sont plus grands que par stimulation monoculaire, ce qui indique une sommation algébrique des effets transmis le long des circuits visuels croisés et décroisés. L'onde *b* de l'ERG est moindre dans le cas binoculaire que monoculaire, ce qui indique une inhibition mutuelle par les fibres centrifuges. La stimulation monoculaire donne aussi des potentiels de l'ERG dans l'oeil non éclairé, quoique beaucoup moindres en amplitude et de polarité contraire. Ces résultats ainsi que d'autres sont confrontés avec les résultats déjà connus dans la littérature.

Zusammenfassung—Die durch monokulare und binokulare Lichtreize erzeugten elektrischen Potentiale wurden gleichzeitig an einer Stelle der optischen Sehrinde der einen Hirnhälfte und an beiden Netzhäuten betäubter Katzen gemessen. Eine Erregung des zur Gehirnelektrode contralateralen Auges führte zu Potentialen mit grösseren Amplituden und kürzeren Zwischenräumen als sie bei Erregung des Auges auf der gleichen Seite auftraten. Die Potentiale bei binokularer Reizung war grösser als die bei monokularer. Das bedeutet eine algebraische Summation der Wirkungen von Erregungen die über gekreuzte und nicht gelöschte Nervenbahnen laufen. Die *b*-Komponente des ERG war

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im binokularen Fall kleiner als im monokularen, was auf eine gegenseitige Hemmung durch centrifugale Fasern schliessen lasst. Monokulare Reize erzeugten ERG Potentiale im nicht gereizten Auge, die jedoch viel schwächer und von entgegengesetzten Vorzeichen waren. Diese und andere Beobachtungen werden in Zusammenhang mit den Ergebnissen aus der Literatur diskutiert.

THIS investigation was undertaken in an attempt to clarify some of the relationships between monocular and binocular photic stimulation and the electric potentials evoked by them in the retina and visual cortex. An interpretation of the findings in the light of present knowledge of crossed and uncrossed pathways and possible mechanisms involved is presented, together with some observations on the recently electrophysiologically demonstrated influences on retinal potentials evoked by photic stimulation.

While the present study was being completed, BURNS, HERON and GRAFSTEIN (1960) published a paper describing experiments similar to ours. Our results agree with theirs wherever experimental conditions were similar, and elaboration of our experiments resulted in some additional findings which are presented.

APPARATUS AND PROCEDURE

Five adult cats (3–3½ kg) were used. A polyethylene cannula was inserted into a femoral vein exposed under ether anesthesia. 1% Pentobarbital was administered through this cannula as necessary throughout the experiment. An average experiment, including surgery, lasted 6 to 8 hr during which time 4 to 6 cm^3 of the drug was given. Saline was infused and the electrocardiograms (ECG) were taken during the experiment.

The head of the animal was fixed in a Baltimore Universal Stereotaxic Instrument. Unilateral (in two cats bilateral) craniectomies were performed with exposure of the upper part of the cerebral hemisphere from the occipital to the frontal pole with lateral extension beyond the suprasylvian gyrus. The dura was cut and reflected. Following infiltration of skin margins with 1% Novocaine the exposed brain was covered with warm mineral oil. After immobilizing both eyeballs by sectioning the extraocular muscles, silverball electrodes, 1 mm in diameter, were applied to both corneae and held in position with sutures to the cut nictitating membrane for electroretinographic (ERG) recordings. The electrocortical potentials were recorded unipolarly with a silverball electrode of 1 mm diameter which was applied to the visual cortex and held by an electrode carrier connected to the stereotaxic instrument. The exact location of this electrode is discussed later. The position of the three electrodes remained unchanged throughout the experiment. The indifferent electrode was placed on the nasion.

For both cortical and retinal recordings a condenser-coupled DuMont Dual Beam Cathode Ray Oscilloscope (Type 333) was used. One of the beams was split into two by means of an electronic switch thus making possible simultaneous recording from three locations. A second oscilloscope with a long-persistence screen was used to monitor traces during experiments. The time constants of the recording channels were equal (about 0·2 sec).

The pupils of the animal were maximally dilated with Atropine sulphate and the lids held apart by sutures or blepharostats. Parallel metal tubes, each 12 cm long and of 12 mm internal diameter, were applied one to each eye. The distance between the tubes coincided with the interocular distance so that both pupils were centered with respect to the aperture of the tubes. Special care was taken to make this arrangement light-tight. Each of the tubes had a fitting shutter to allow stimulation of each eye separately. Light tightness of the

system with both covers closed was checked by showing the absence of retinal and cortical potentials following photic stimulation. The animal was kept in the dark during the experiment.

A Grass Photo Stimulator (Model PS–1) was used. This stimulator provides five different intensities of which the highest (setting 16) is sixteen times more intense than the lowest. To extend the intensity range further, a series of neutral-density filters was used, which provided a total range of about six log units. All intensity steps were related to setting sixteen of the stimulator with no filter applied. The flash duration was about 10 μsec. The flash-lamp provided diffuse light and was covered with a light-tight metal plate with a

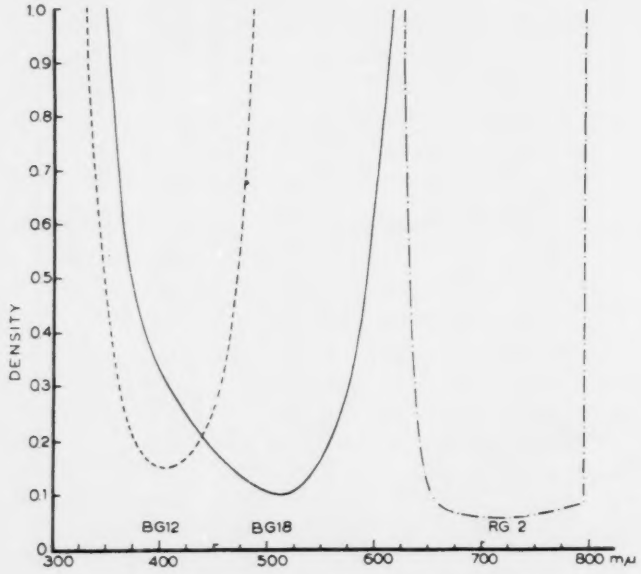

FIG. 1. Density curves for Schott color filters.

rectangular opening which served as filter holder. Since the flash-lamp contained a parabolic reflector, the two tubes were in line with the reflected parallel rays of light. All upward deflections in the recordings are surface-positive, both in retinograms and corticograms.

A Grass Kymograph Camera (Model C–4E) was used to record eighty superimposed oscillograph traces on one frame. The sweep was synchronized to start at the time of stimulation which was marked with a pip in the upper beam.

The light used for stimulation was either the unfiltered light of the xenon-filled tube or chromatic light of short, short plus medium, or long wavelengths. The unfiltered light was bluish-white, and was used over an intensity range of about six log units. It is referred to as white light in the text for brevity. The highest intensity of the filtered chromatic light was of lower absolute level than that of the unfiltered light because of absorption in the filters and the restricted energy available in the light source.

Wratten neutral-density and Schott color filters (BG 12, BG 18 and RG 2) were employed. The spectral density of all neutral and color filters was calibrated with a Cary spectrophotometer in the range of 300 mμ to 800 mμ (Fig. 1). The energy scale used in these

experiments was relative and log 0·0 represents highest energy available in the unfiltered white light. The intensity of the light transmitted through the filters was measured relative to that of the white light.

The animals were kept in the dark for 20 min following completion of surgery and prior to the beginning of the experiment. Sixty-two sets of three experiments each were carried out in the following sequence: Eighty superimposed records of cortical and retinal potentials after binocular stimulation at a rate of one per second were followed by a similar record with right and another with left monocular stimulation. A dark interval of 5 to 10 min was allowed between each triple sequence of stimulation.

The procedure for evaluations of the records was as follows:

1. An average curve was prepared from each of the superimposed cortical recordings by free-hand tracing with the aid of a magnifier. All these average curves were drawn by the same person, and were reproducible by him. After measuring the amplitudes of each average cortical response curve along the x-axis in steps of 6·25 msec, the left and right monocular curves were added to each other. The resulting summated curve was superimposed on the average trace obtained from the record after binocular stimulation.

2. Latency measurements were made from onset of stimulation to the peak of the first positive and the peak of the first negative deflection in the case of the electrocorticograms (ECOG) and to the peak of the first negative (*a*-wave) and the peak of the positive elevation (*b*-wave) in the case of the electroretinograms (ERG).

3. Amplitudes were determined in the electrocorticograms and retinograms by measuring the vertical distance between the peaks of the first positive and the first negative deflections.[3] When in corticograms the first positive, and in retinograms the first negative peak was not visible in records taken at lower intensities of stimulation, the point at which the trace just swings off the base line was used.

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RESULTS

In preliminary experiments we investigated the response of different areas of the sensory cortex to photic stimulation with white light of medium and high intensities. Our results were in agreement with those of other workers (MARSHALL, TALBOT and ADES, 1943; DOTY, 1958), showing that potentials evoked by photic stimuli are not restricted to the striate area of the occipital lobe. It appears from our recordings that potentials can be evoked from the whole sensory cortex. However, the potentials evoked in the striate area and close vicinity (parastriata) differ characteristically from those evoked in the rest of the sensory cortex.

The response common to all parts of the sensory cortex was a surface-negative deflection with a consistent peak latency. In most of the striate cortex and its close vicinity this potential was of much greater amplitude and was preceded by a sharp positive spike. The response in the striate area was further characterized by a number of additional later waves which lack the consistency displayed by the first negative deflection with respect to its peak latency and amplitude with change of the stimulus condition on the one hand and with change of the cortical position of the electrode on the other. Moreover, these long-latency deflections differed from animal to animal which was not the case with the first negative potential.

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[3] Several investigators measure the amplitude of the first negative potential of the corticogram from its peak to the peak of the following positive wave.

Because of the characteristic difference between the response of the striate area and the extrastriate areas, and the consistency of the first negative potential, the electrode was placed in a mid-striate position on the optic cortex (Fig. 2) and only the first negative potential was evaluated in terms of its amplitude and latency as function of the intensity of stimulation.

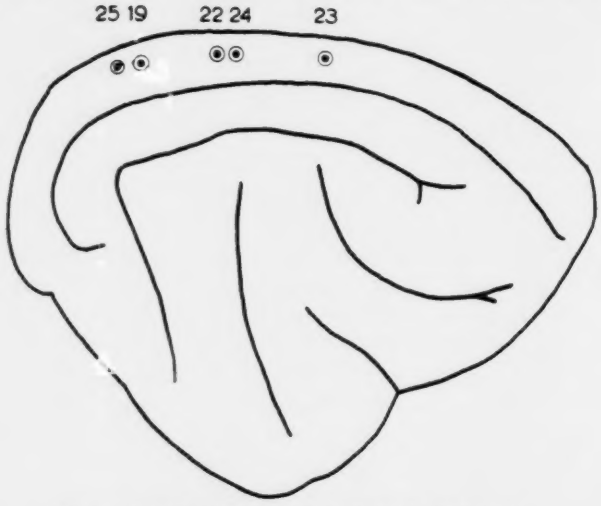

FIG. 2. Localization of cortical electrodes in five cats.

The cortical response to photic stimulation consists of a complex wave with peak latencies between about 10–15 msec and 110 msec measured from the first positive peak up to the last. This is very different from the response to electric stimulation of, for instance, the optic nerve (MARSHALL, TALBOT and ADES, 1943; BISHOP and CLARE, 1955; MALIS and KRUGER, 1956; CHANG, 1956; LENNOX, 1958; DOTY, 1958), which consists of a succession of four positive peaks of which the first appears after less than 1 msec. This latency is not very far from values of the retino-cortical time derived from records after photic stimulation (Table 1).

TABLE 1

	Retinal Time/msec (4 log units)	Cortical Time/msec (4 log u) (5 log u)	Retino-cortical Time/msec (4 log units)
White stimulation:			
binocular	11 –26	12·5–29 –37·5	1·5–3
ipsilateral	10 –27	14·5–31·5 –39	2·5–4
contralateral	10 –26	13 –28·5 –37·5	2·5–3·5
Blue stimulation (BG 12):			
binocular	11 –25·5	14 –29·5 –38	4 –5·5
ipsilateral	10·5–27	15·5–33 –40	5 –8
contralateral	11 –25	15 –31 –39	4 –6·5
Blue-green stimulation (BG 18):			
binocular	11 –24·5	13·5–27·5 –37	2·5–4·5
ipsilateral	11 –23·5	15 –29 –37	4 –6
contralateral	11 –23	13·5–27·5 –37·5	2·5–5

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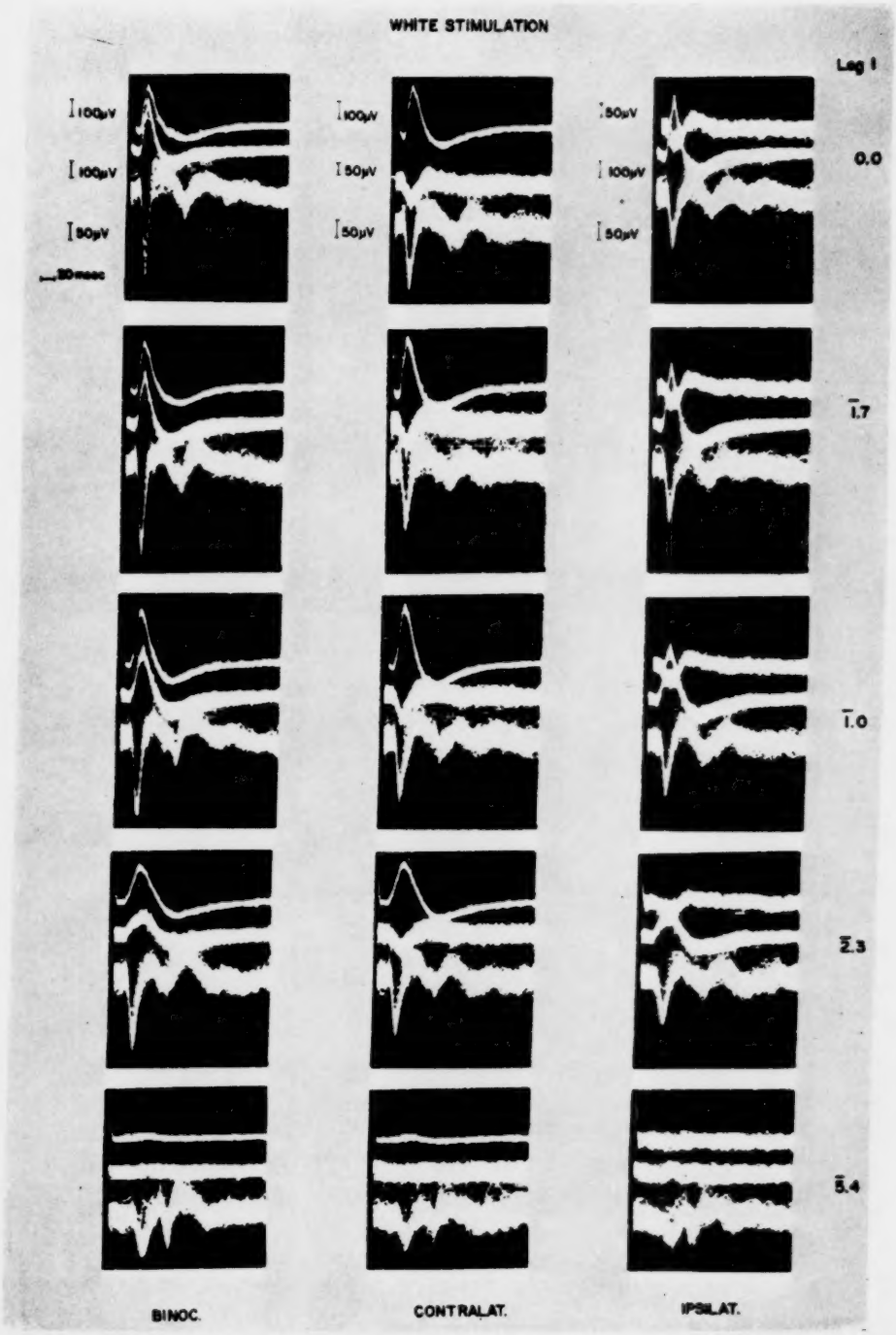

FIG. 3. Retinal and cortical potentials following stimulation with white light of five decreasing steps of intensity (Cat 25).

upper beam: right ERG
intermediate beam: left ERG
lower beam: Corticogram

left column: binocular stimulation
intermediate column: contralateral stimulation (right eye)
right column: ipsilateral stimulation (left eye)

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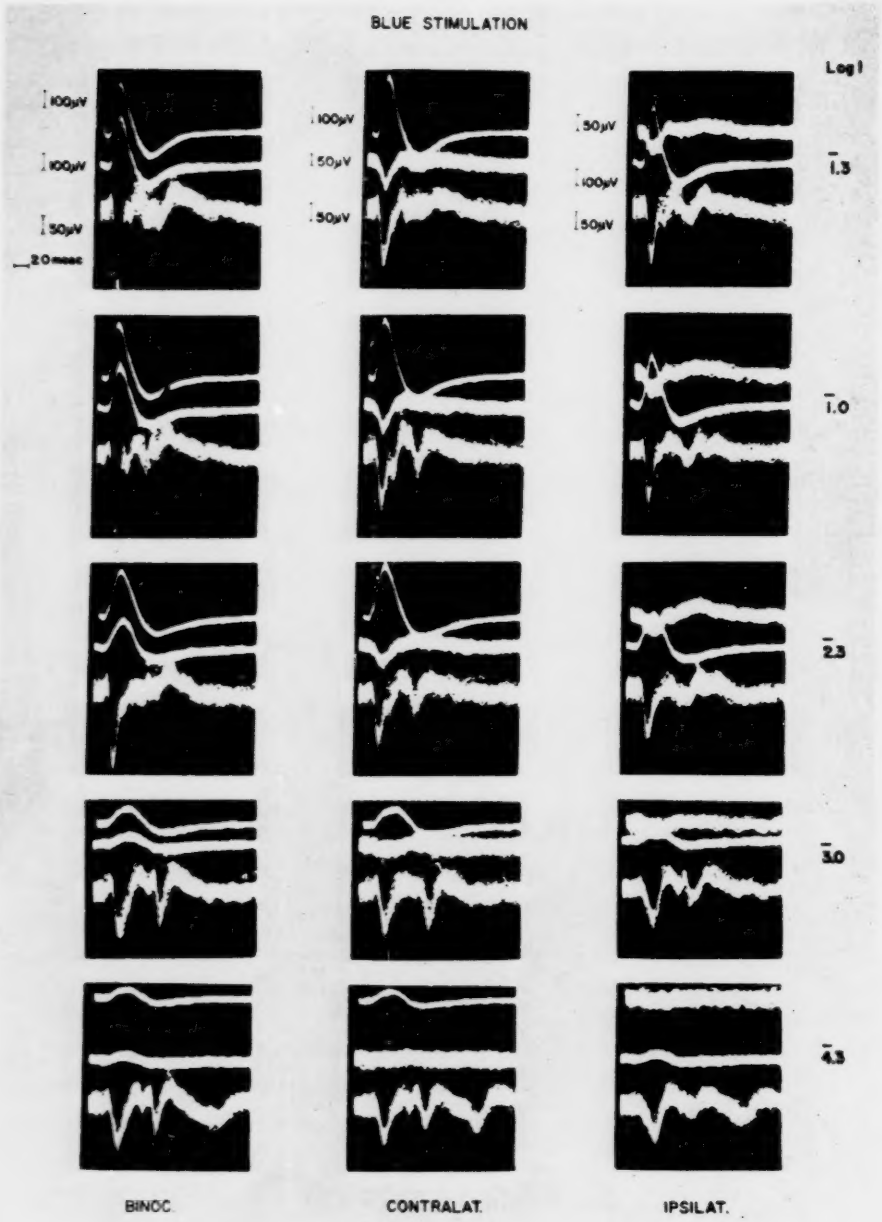

FIG. 4. Same as Fig. 3 with blue light (BG 12).

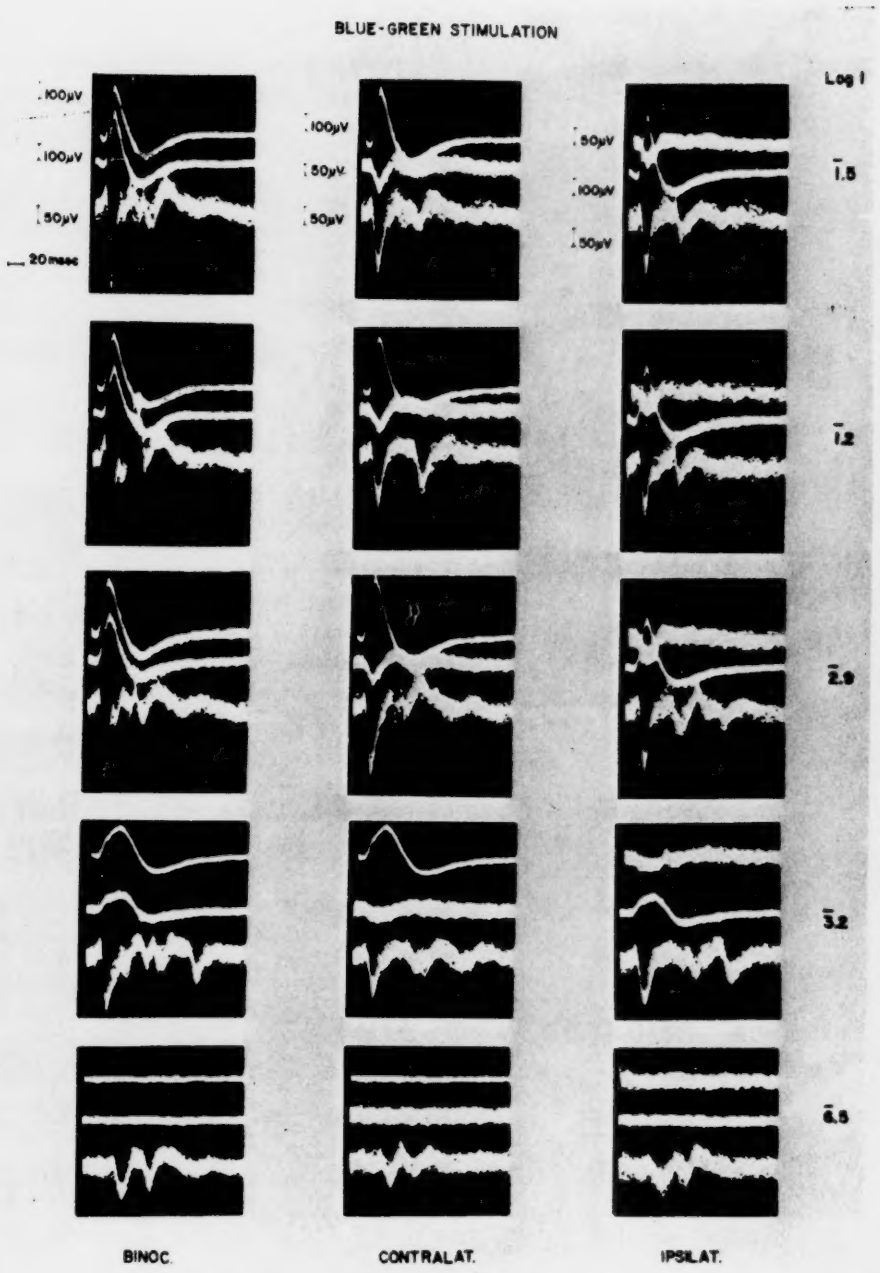

FIG. 5. Same as Fig. 3 with blue–green light (BG 18).

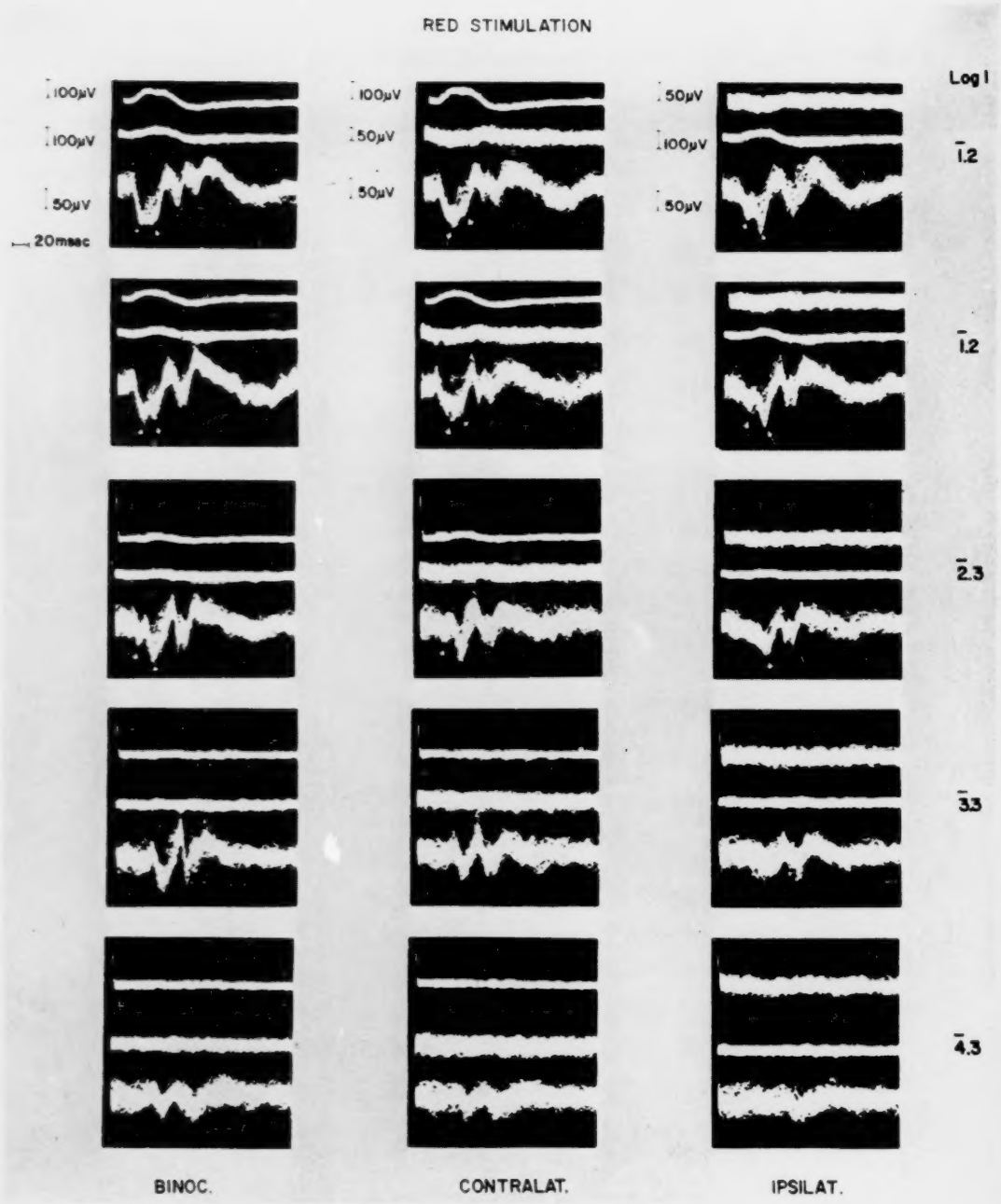

FIG. 6. Same as Fig. 3 with red light (RG 2).
The arrows indicate the first and second components of the first negative deflection of the corticogram.

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Using white and colored light, striate responses to monocular stimulation, both contra- and ipsilateral, were smaller in amplitude than those to binocular stimulation and the wave pattern was generally less complex (Figs. 3–6). The difference between the two monocular responses is most striking. In all experiments the cortical response to stimulation of the contralateral eye was greater in amplitude and more complex in form than that following stimulation of the ipsilateral eye. Moreover, the latency, measured at the peak of the first negative deflection, was shorter for contralateral than for ipsilateral impulses, a difference which became more marked as stimulus strength decreased. Thus, the cortical response to contralateral stimulation is the dominant component of the response to binocular stimulation with respect to amplitude; it also precedes the ipsilateral response. Since no precise information is available regarding the length of the afferent pathways involved, conduction velocity cannot be calculated.

A comparison of the algebraically summated response curves of both individual monocular stimulations, with the experimentally observed binocular response curve to different intensities of white light, is presented in Fig. 7.

The striate response to binocular or monocular stimulation increased in amplitude with increasing intensity of light up to a certain level and then either declined or remained constant despite further increase in intensity within the limits of our experiment (Figs. 7 and 8).

This relationship between amplitude and stimulus strength was marked for white and blue-green light (BG 18), but was only just noticeable for blue light (BG 12). In the case of red light (RG 2), the response to which had two components (to be discussed later), the effect was seen only in the second component of the first negative deflection. Reasons for this limitation have been given before. The amplitudes of the potentials evoked by red light were much smaller than those evoked by other colors, and therefore were only measurable for a short range of intensities.

Thus, maximal striate response did not coincide with maximal stimulus strength. An inhibitory effect was displayed by an intensity above a certain level no matter whether stimulation was applied binocularly or monocularly, and irrespective of which color was used; it is therefore independent of the wavelength.

Peak latency decreased almost linearly with increase of log intensity without any deviations at highest intensities. The linear course of the latency curves was practically the same for all test lights after binocular and contralateral stimulation with perhaps a slight tendency for the blue-green response to be shorter and for the first component of the red response to be longer. However, ipsilateral connexions appeared to discriminate to a greater degree than contralateral connexions with regard to peak latencies for different qualities of stimulation; here latency was distinctly longest for red and white, shortest for blue-green and intermediate for blue stimulation. In general, activity propagated along ipsilateral pathways took a longer time to arrive at the cortex than activity propagated along contralateral pathways (Fig. 8, right).

There were certain differences between cortical responses to white and colored light (Figs. 3–6).

Responses to all lights used except red had a common characteristic consisting of a large first negative deflection preceded by a short positive spike, and followed by another smaller negative deflection. The latency of this late peak in the response varied in the different animals relative to the first peak and to the onset of the response curve. In the example of Cat 25 it was about 60–75 msec. Whereas the latency of the first negative deflection lengthened

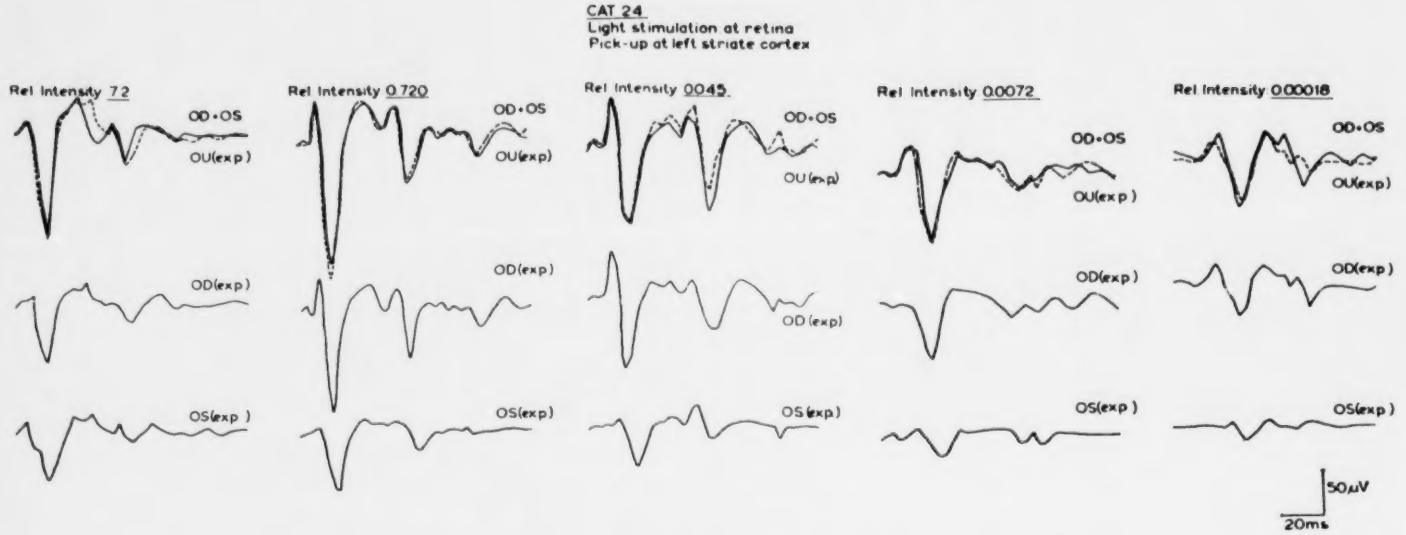

FIG. 7. Tracings of average cortical electric responses to white light stimulation (Cat 24).

Full lines: Upper tracing: binocular stimulation
Intermediate tracing: contralateral stimulation
Lower tracing: ipsilateral stimulation

Hatched lines in upper tracings: "binocular" summated curves from responses to contralateral (intermediate tracing) plus ipsilateral stimulation (lower tracing).

Relative intensity 7·2 corresponds with log 0·0.

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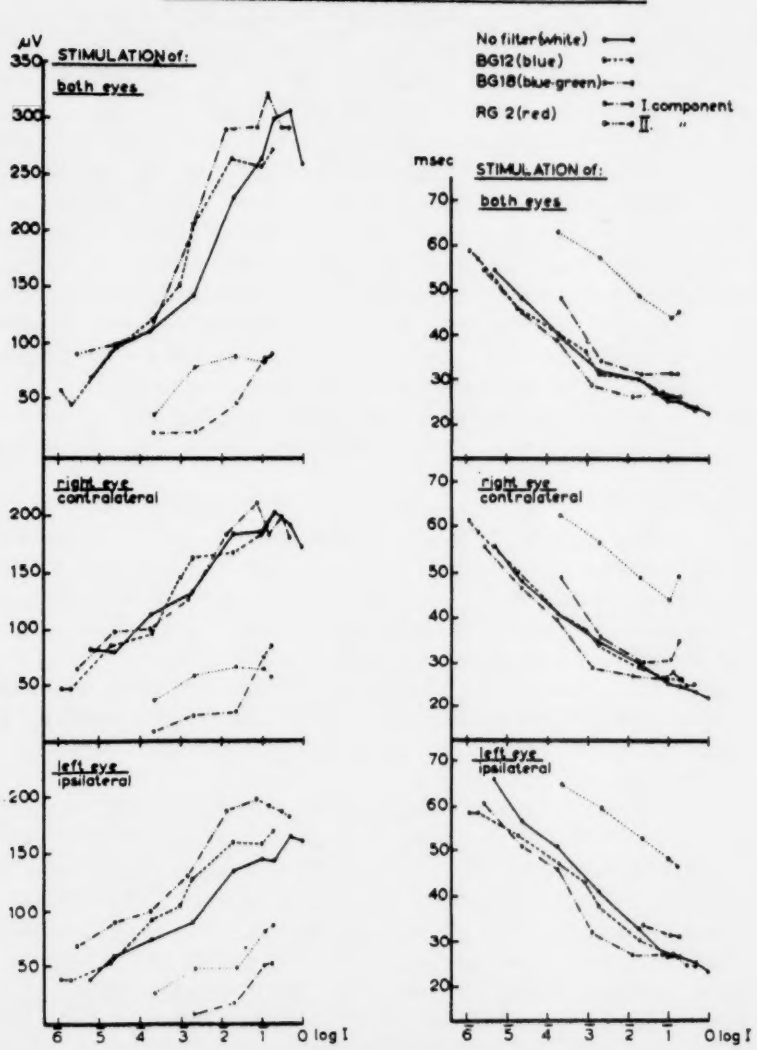

FIG. 8. Measurements of potentials of striate cortex.

left: amplitudes of first negative (downward) deflection measured from preceding positive peak.
right: peak latencies of same wave measured from onset of stimulation.

and its amplitude decreased considerably over the intensity range of six log units, there was very little change in the latency and amplitude of the second negative deflection over this range. This applied to all stimulations with the exception of the ipsilateral white at lowest intensity (not shown in the figure), where both negative deflections fused to an apparently single wave with a peak between the first and the second wave appearing at higher stimulus strength.

The response to blue (BG 12) and especially to blue-green light (BG 18) showed additional small deflections between the first and second larger peaks (Figs. 4 and 5).

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Attention is drawn to the difference in potential of the responses evoked by the different test lights (Fig. 8, left). Highest amplitudes were obtained over the intensity range after binocular and ipsilateral stimulation with blue-green light. They were somewhat lower with blue and still lower with white light, whereas amplitudes did not differ much following contralateral stimulation with the different test lights. Differences in amplitude consequent to differences in the color of lights used were greatest in the case of ipsilateral stimulation.

Red light evoked much lower potentials than the other colors at equal energy (Fig. 6). The responses produced a long-latency multiwave pattern and a splitting of the first negative deflection into two components of which the first one almost tallied with the first negative potential after white and blue stimulations. The first component was less sensitive since it was evoked only by high-intensity stimulation when it was most prominent upon stimulation of the contralateral eye, while the second component was more prominent after stimulation of the ipsilateral eye. This behavior is in keeping with the shorter peak latency for contralateral stimulation. The retinograms resulting from stimulation with red light were of very low potential compared with those elicited by stimulation with other test lights at equal energy. They showed a distinct two-component pattern of the positive potential at highest intensity.

The outcome of this experiment induced us to check for the presence of such a second component of the first negative deflection in our recordings. In fact, a small and often indistinct second negative wave was found in several of them. It may have been masked in other cases by the first high-amplitude component and by base line fluctuations.

Therefore, actual measurements for both components are only given for recordings made after red stimulation where its presence was not masked (Fig. 8).

Despite an attenuation of intensity of about six log units for all stimulations except red, the amplitudes of evoked potentials decreased only by a factor of not more than six to one. This discrepancy between the ranges of the physical and the physiological factors probably makes vision both possible and efficient.

A measurable electroretinogram (ERG) could only be obtained over a range of approximately four log units. The retinal response consists essentially of the negative *a*-wave (downward deflection) and the positive *b*-wave. Both waves include photopic and slower scotopic elements which show in some recordings as small ripples. Detailed measurements of such additional potentials were not made. According to Granit's analysis, the *a*-wave is considered to be the result of the activity of inhibitory elements (P III, negative polarity) which are faster in their response to stimulation than excitatory elements (P II, positive polarity) (GRANIT and THERMAN, 1935). The discharges of the excitatory elements are propagated along the optic pathways to the brain (GRANIT, 1947). Thus, the peak of the *a*-wave practically represents the beginning of the retinal excitatory event, or rather the point at which it makes its presence seen and serves thus as a measure of the latency of the retinal excitatory event. The amplitude of the *b*-wave is therefore usually measured from the peak of the *a*-wave.

MONNIER (1952) measured the time which elapses between the peak of the *a*-wave of the ERG and the start of the evoked response wave in the cortex and called it the Retino-cortical Time. For this purpose he determined the peak latency for the *a*-wave (Retinal Time) and the start of the cortical response (Cortical Time) both from the onset of stimulation and calculated the difference between both latencies. We were unable to make similar measurements from our records owing to the width of the base line which usually masked the beginning of the cortical response. We therefore decided to measure the time which

elapses between the peak of the *a*-wave in the ERG and the first distinct positive peak in the corticogram which precedes the large characteristic negative deflection.

The results obtained are presented in Table 1 and in Fig. 9. The Retinal Time increased from 10 msec to 27 msec over an intensity range of about four log units. It was practically the same for white and blue (BG 12) stimulation and perhaps slightly shorter for monocular stimulation.

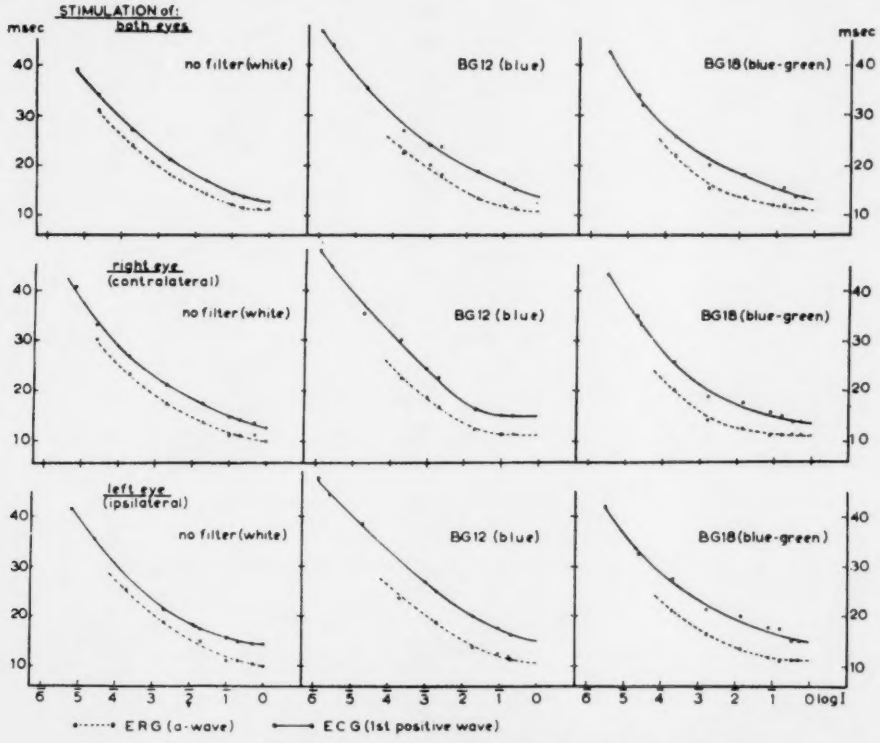

FIG. 9. Retinal and Cortical Time: dotted lines—electroretinograms (*a*-wave).
full lines—electrocorticograms (first positive wave).

A similar but greater increase of peak latency was seen for our criterion of the cortical excitatory event with decreasing intensities over a range of four log units. The time was from 12·5 to 29 msec for white stimuli with a distinctly longer period for ipsilateral conduction (14·5–31·5 msec). Binocular and contralateral stimulation had practically the same latency. Our cortical time for binocular and both monocular stimulations was shortest for blue-green (BG 18), slightly longer for white and longest for blue (BG 12) stimulation.

The Retino-cortical Time derived from our two criteria was shortest for binocular white stimulation (between 1·5 and 3 msec depending on the intensity of stimulation) and longest for ipsilateral stimulation with an increase from 2·5 to 4 msec over the same range of four log units. The longest retino-cortical time was obtained with blue and the shortest with white light. The accuracy of these measurements at low intensities was seriously limited owing to the ill-defined *a*-wave and the width of the base line in the corticograms.

As at the striate level, maximal retinal response to photic stimulation (measured at the peak of the *b*-wave) did not coincide with maximal stimulus strength (Fig. 10). The graphs

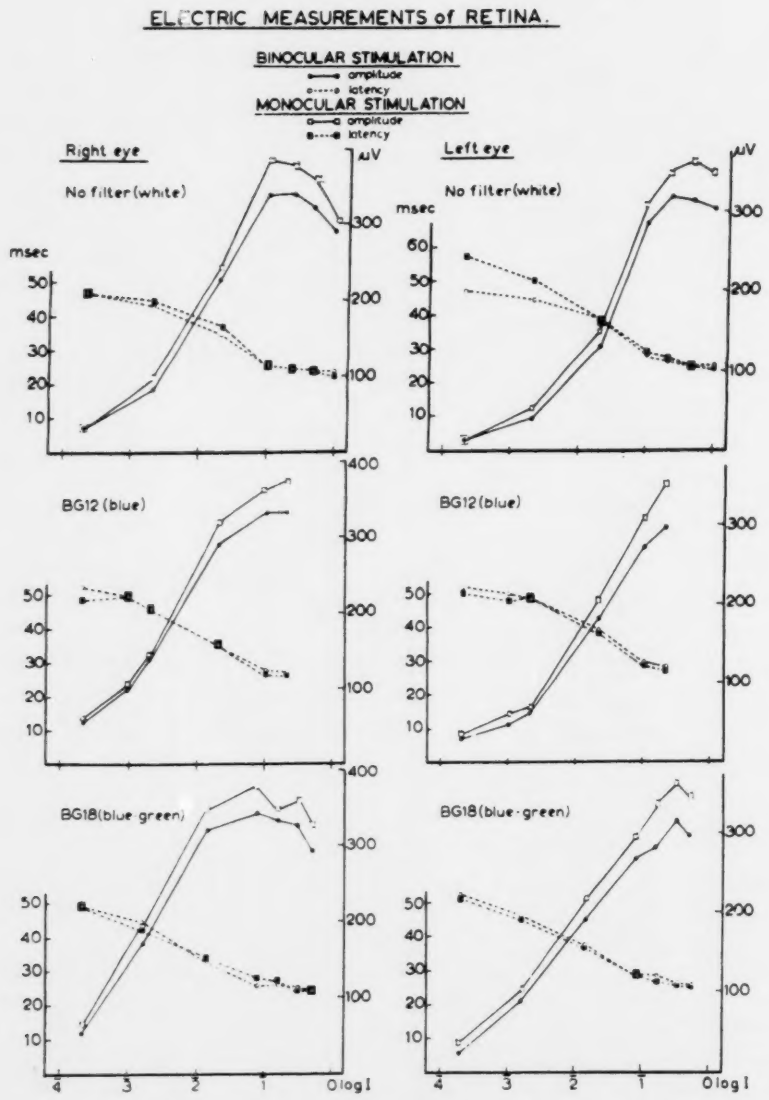

FIG. 10. Electric measurements of retina. Amplitudes and latencies refer to the *b*-wave.

show that the amplitudes of the retinal responses to monocular and binocular stimulation increased linearly with increase of log intensity up to a certain stimulus strength and then either levelled off or declined. This levelling off and decline covered a range of one to two log units for white and for blue-green stimulation. For blue light at highest intensities the amplitude curves only flattened slightly but might have shown a decline if light of higher intensity had been available.

The peak latency of the *b*-wave decreased almost linearly as log intensity increased over the whole range.

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The *b*-wave of the ERG elicited by monocular stimulation was always of greater amplitude than the corresponding *b*-wave after binocular stimulation.

The electric response to monocular stimulation was not restricted to the stimulated eye. Although in the dark, the other retina also responded. Its response differed from the ERG of the stimulated eye in that its polarity was reversed and its amplitude was much smaller (Figs. 3–6), necessitating an increase in the gain of the recording channel. The amplitudes of these reversed responses decreased when stimulus strength was lowered. This effect has been further investigated and the results will be published in a forthcoming paper.

DISCUSSION

The first negative deflection of the cat's cortical response to photic stimulation could be recorded from all parts of the sensory cortex. This is unlike the situation in the rabbit (O'LEARY and BISHOP, 1938a, b), and the monkey (DOTY, 1958), where correspondence could be demonstrated between histologically defined striate area and optically excitable cortex. Our findings suggest that the striate layer responsible for the first negative potential in the cat either possesses lateral synaptic connexions which interconnect the visual cortex with the other sensory areas, or that there is a lateral spread of optic nerve collaterals which interconnect the lateral geniculate body with sensory areas other than the striate one. O'LEARY (1941) provided some evidence that ascending optic nerve fibers in the visual cortex of the cat may give off long horizontal branch fibers which extend to neighboring areas.

BURNS, HERON and GRAFSTEIN (1960) evoked potentials in the unanesthetized cat's visual cortex by photic stimulation and found that "surface responses produced by stimulation of the contralateral eye are larger in amplitude than those produced by stimulation of the ipsilateral eye, while those produced by binocular stimulation are larger still". Our experiments with anesthetized cats confirm their findings. We agree with these authors that one way to explain this phenomenon is to assume that the uncrossed pathway of the cat's visual system is of smaller diameter than the crossed, which means that it consists of a smaller number of individual fibers; this would imply a wider cortical projection of the crossed connexions. This view is supported by Bishop, Jeremy and Lance's electrophysiological (and histological) demonstration that a majority of the fast conducting fibers decussate, displaying greater amplitudes of potentials than any other fiber group in both pathways. However, no clear-cut anatomical confirmation of this experimental result can be obtained from the literature; on the contrary, an approximately equal overall diameter for both pathways in the cat is generally presumed (LEGROS CLARK, 1942; POLYAK, 1957). Yet, electrophysiological findings appear to give some indication of the anatomical relations.

Our measurements show that the cortical response to binocular stimulation results from the linear summation of the electromotive forces of cortical responses to both monocular stimulations. In other words, upon simultaneous stimulation of both eyes cortical potentials produced by impulses propagated along contralateral pathways sum algebraically in the visual cortex with cortical potentials produced by impulses propagated along ipsilateral pathways. This is true for all our experiments of which one example is presented in Fig. 7.

The latency of the cortical effect was found to be greater via the nondecussating pathway than via the decussating one (Fig. 8, right), an effect which has also been reported by DOTY (1958) and by BURNS *et al.* (1960). The velocity of conduction of impulses along these pathways cannot be calculated from these latency measurements since the exact length of

the two pathways and the synaptic delay is not known; there even appears to be some evidence that the crossed pathways are longer than the uncrossed ones (BISHOP *et al.*, 1953).

The longer latency of the ipsilateral cortical effect may in our opinion be accounted for by the data of BISHOP *et al.* (1953) who showed that the majority of uncrossed optic fibers are of small diameter and therefore conduct impulses more slowly than the crossed optic connexions which contain a majority of thick fibers. The clear resolution of the first negative deflection into two components with high-intensity red light (Fig. 6), which occurred to a lesser extent in some other records, suggests the possibility that this negative potential is always compounded of two components with different latencies. These different latencies may reflect different rates of conduction in two groups of fibers of different diameter.

The different latencies of the cortical response obtained under various experimental conditions could also be interpreted in terms of differing synaptic delays in the peripheral organs, the lateral geniculate body, or the cortex. No evidence for or against this possibility can be offered at present. The increase in latency may also be due to branching of the afferent fibers close to the cortex reducing the fiber diameter.

The fact that the ipsilateral potential is smaller than the contralateral potential is difficult to explain in terms of afferent pathways. The greater proportion of small fibers in the ipsilateral pathway (BISHOP *et al.*, 1953) would be expected to result in larger potentials in the ipsilateral record, since a greater total number of fibers should then be present assuming the overall diameter of both pathways to be equal. This, however, does not account for experimental facts. On the contrary, as mentioned above, there is electrophysiological evidence from the work of Bishop *et al.* to the effect that the decussating pathway consists of a majority of thick fibers whose potentials are greater than the potentials measured from all other fiber groups in both pathways. It may be assumed that these thick fibers are present in such a majority that they determine the higher amplitudes of the wave pattern of the cortical response to contralateral stimulation.

The fact that the first component in the red response is larger when the contralateral eye is stimulated, and the second component larger when the ipsilateral eye is stimulated, is in accordance with this interpretation. This, however, leaves open the question as to why the first component of the red response is less sensitive than the second. Since this component appears to correspond with the first negative deflection following stimulation with other test lights, the explanation of this effect may be that the cat's visual system is less sensitive to long-wave light than to other wavelengths, a fact which shows also in the low-amplitude cortical and retinal responses.

Records (Figs. 3–5) and corresponding curves (Fig. 8) show that the amplitude of the first negative potential increases linearly when plotted against a logarithmic scale of increasing stimulus intensities, while the corresponding peak latencies decrease linearly. Above a certain level of intensity, the amplitudes of the cortical responses either remain constant or diminish. This is in agreement with curves from the work of LENNOX and MADSEN (1955), MADSEN and LENNOX (1955) and INGVAR (1959).

An inhibitory effect of light of high intensity is displayed at the retinal level where HARTLINE (1938) demonstrated reduction of the frequency response of single optic nerve fibers in the frog above an optimal light intensity. This effect could later be traced in part to antagonistic and inhibitory elements among the receptors of retinal receptive fields feeding single ganglion cells (KUFFLER, 1953; BARLOW, 1953; HARTLINE, WAGNER and RATLIFF, 1956). This phenomenon has also been demonstrated by the use of the threshold criterion of the critical frequency of fusion both electrically in individual ganglion cells of the rabbit's

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retina (DODT, 1956b) and in human psychophysical measurements. Our retinographical recordings (Fig. 10) show this phenomenon by the fact that amplitudes of the *b*-wave of the ERG decrease when a certain level of stimulus strength is surpassed (see also GRANIT, 1947).

Thus, inhibition already occurs in the retina. However, as our graphs show, inhibition is seen in the cortical records as well (Fig. 8). From our results it cannot be concluded with certainty whether the cortical inhibition is only the consequence of the retinal inhibition or a phenomenon in its own right. However, in view of the findings of JUNG, VON BAUMGARTEN and BAUMGARTNER (1952), JUNG and BAUMGARTNER (1955), BAUMGARTNER (1955), and BAUMGARTNER and JUNG (1955), which demonstrate the presence of inhibitory mechanisms in single cortical neurons, inhibition may also be occurring at the cortical level.

The effects of afferent impulses from simultaneous stimulation of both peripheral organs summate in the cat's visual cortex. There is also another site of interaction of the two retinae within the brain.

Our recordings and graphs (Figs. 3–6 and 10) show that the retinal responses, measured at the *b*-wave, are always smaller after binocular than after monocular stimulation. This effect was observed in the human eye by WIRTH (1951) but denied by UCHERMANN (1955). A year later, MOTOKAWA, NAKAGAWA and KOHATA observed in human subjects that the ERG to binocular stimulation displayed a deep afterswing of the declining branch of the *b*-wave which was not present following monocular stimulation. This effect was not present in our recordings from the cat's retina.

Since there is no evidence for the existence of a direct nervous connexion between the retinae, the simultaneous inhibition of both retinal potentials following binocular stimulation must be mediated through central pathways. Binocular stimulation elicits a response in the optic cortex that is delayed by at least 1·5 msec. An impulse returning from the cortex to the retina would arrive there too late to exert an inhibitory influence on the excitation in the retinae. This reasoning suggests that the origin of this inhibitory effect is at a central level lower than the cortex.

The negative retinal response of the dark eye following photic stimulation of the other eye was regularly observed (Figs. 3–6). This phenomenon may be the expression of an inhibitory effect from the central nervous system. It is therefore related to the problem of biretinal association and will be given fuller treatment at a later date.

Centrifugal fibers which might be involved in these phenomena have been described from histological preparations of retinae and optic nerves of the bird (RAMÓN Y CAJAL, 1889; DOGIEL, 1895), of the dog (RAMÓN Y CAJAL, 1894) and of the chimpanzee (POLYAK, 1957). Further evidence for their existence has been derived from nerve fiber degeneration experiments in the rabbit (VON MONAKOW, 1889). Finally, there is electrophysiological evidence of such efferent fibers. GRANIT (1955) showed that in the cat electric stimulation (tetanization) in the reticular formation of the tegmentum potentiates or inhibits responses to light of single ganglion cells which were not excited antidromically. DODT (1955, 1956a) came to a similar conclusion from his work with rabbits. In stimulating the optic tract with single shocks contralateral to a single retinal ganglion cell from which he recorded, he obtained a small spike which was consistently delayed, relative to antidromic spikes of very short latency. Since this delayed spike could not be elicited by light stimulation, he concluded that it was produced by impulses in centrifugal fibers. There is furthermore MÜLLER-LIMMROTH's finding (1954) in the guinea-pig where a retinal response occurred in the dark eye of the same polarity as the ERG in the other eye following stimulation with white and

colored lights. He showed that this consensual effect in the dark eye is extinguished after sectioning of either optic nerve and after elimination of the lateral geniculate body of the same side as the dark eye. He concluded that centrifugal fibers are responsible for the consensual effect which thus runs from each lateral geniculate body to the ipsilateral retina.

Our results demonstrate mutual inhibition of the responses of the two retinae, which are under constant reflex control of the central nervous system. Thus, the retinal response, though originating in the retina, appears to be regulated by feedback from the contralateral retina via the central nervous system before sending its coded message to the cortex.

SUMMARY

Electric potentials evoked by photic stimuli were measured simultaneously at one position on the visual cortex of one hemisphere, and at both retinae in anesthetized cats.

White, blue, blue-green, and red light flashes were used over an intensity range of six logarithmic units. The stimulus was applied to both eyes simultaneously and to each eye separately and measurements were made from photographic superimpositions of eighty individual sweeps.

Cortical responses to right and left monocular stimulation differed from each other and from the response to binocular stimulation, irrespective of the color and intensity of the light. Stimulation of the eye contralateral to the cortical electrode produced potentials with greater amplitudes and shorter latency than the potentials evoked by stimulation of the ipsilateral eye. Potentials evoked by monocular stimulation of either eye were smaller than those evoked by binocular stimulation.

Addition of the electromotive forces of the individual monocular curves resulted in a curve which closely fitted the bioelectric cortical response to binocular stimulation. Thus, the cortical response to binocular photic stimulation represents an algebraic summation of the effects of activity conducted along the crossed and uncrossed visual pathways in the cat.

Monocular stimulation of either eye evoked electroretinograms with larger positive deflections (*b*-wave) than following binocular stimulation. This phenomenon demonstrates neural interconnexion between both eyes and mutual inhibition of the electric responses of the two retinae. The retinal effect is presumed to be brought about by sub-cortical control via centrifugal fibers.

Monocular stimulation elicited an electric response in the dark eye as well. This response is in the cat of reversed polarity and of much lower amplitude than the electroretinogram elicited in the stimulated retina.

Up to a certain level of intensities amplitudes increased linearly and latencies decreased linearly with log intensity. Stimulation above this level of intensity produced an inhibitory effect both in the retinal and in the cortical response; it elicited potentials the amplitudes of which levelled off and sometimes decreased with further increase of intensity, while latencies continued to decrease.

The retino-cortical time was determined for the different kinds of stimulation used with the exception of red. The criterion taken was the difference in latency between the first peak of the electroretinogram (negative *a*-wave) and the first appearing peak in the electrocorticogram (first positive peak, or if not measurable at lower intensities the turning point of the base line to the first negative wave). Within the intensity range employed the retino-cortical time was shortest for white, blue and blue-green test lights after binocular and contralateral stimulation with a slight tendency to be still shorter for the binocular. The retino-cortical time was shortest after white and longest after blue stimulation.

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NOTES ON THE PHOTOMETRIC SIGNIFICANCE OF THE HUMAN CRYSTALLINE LENS

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Abstract—The effective pathlength of the human crystalline lens is calculated as a function of aperture and its photometric effects examined on the assumption that the distribution of yellow pigment is uniform. The data are applied to the interpretation of the age variation of the absolute visual threshold and to the spectral variation of the Stiles–Crawford effect.

Résumé—On calcule l'epaisseur effective du cristallin humain en fonction de l'aire pupillaire et on examine les effets photométriques en présumant que la distribution du pigment jaune soit uniforme. On emploie les résultats pour interpréter la variation du seuil absolu en fonction de l'âge et aussi la variation spectrale de l'effet Stiles–Crawford.

Zusammenfassung—Die effektive Dicke der menschlichen Linse wird als Funktion der Pupillenweite berechnet und ihre photometrische Bedeutung unter Annahme der gleichmässigen Verteilung des gelben Pigmentes bewertet. Die Angaben werden zur Erklärung der Altersfunktion der absoluten Schwelle und der Spektralverteilung des Stiles–Crawford Effektes benützt.

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1. INTRODUCTION

THE interpretation of visual experiments involving measurements of radiance depends on a knowledge of the transmission characteristics of the pre-retinal media. More than 50 per cent of the incident energy in the violet and blue part of the spectrum is absorbed by the crystalline lens alone. LUDVIGH and MCCARTHY (1938) were the first accurately to measure the transmissivity of human pre-retinal media in excised eyes and SAID and WEALE (1959) studied the spectral properties of the living human lens as a function of age. Rather remarkably, it seems to have been implicitly ignored that the crystalline lens is lens-shaped. Its effective pathlength is longer when the pupil is constricted than when it is dilated and one wonders whether this difference is important and, if so, what consequences one has to draw from this consideration.

The spectral properties of the lens are very peculiar, e.g. the neo-natal lens is characterized by the presence of yellow pigment in concentrations usually found only in old lenses. This pigment disappears in the first year or two of life (HOSOYA, 1929; SALMONY and WEALE, 1959) and the same or another pigment starts accumulating again after puberty. The simplest assumption one can reasonably make in a consideration of the effective pathlength of the lens is that the light-absorbing substance uniformly permeates the lens matrix. This may be true for young and middle-aged lenses but is not necessarily applicable to older lenses which, on account of metabolic difficulties, may reveal an accumulation of one or more such substances in the nucleus (WEALE, 1954, 1960). Repeated efforts to detect some systematic

variation by photographing excised human lenses in blue and yellow light have been disappointing. It would appear that the only lenses which are optically sound are those *in situ* and, for reasons which need not be here discussed, scanning the lens with a narrow beam has not so far been practicable. In the following, then, we shall make the assumption that the lens matrix is uniformly pigmented: it will be readily appreciated that such corrections as will be derived provide a lower, not an upper, limit.

2. THEORY

As the meridional section of the human crystalline lens is not easily described by an algebraic expression, an estimate of the mean pathlength as a function of aperture is

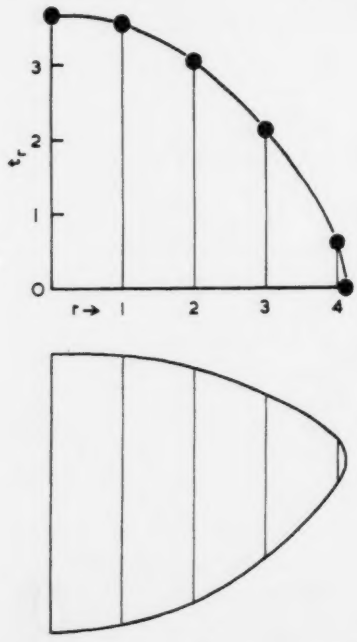

FIG. 1. Bottom: Section through human lens. Top: Geometrical pathlength as a function of distance from the centre. Scales in mm.

achieved most readily by graphical means. In the computation use was made of a diagram of the capsule (FINCHAM, 1937) traced on sectional paper. Clearly, the mean pathlength $\bar{x}$ is given by

$$\bar{x} = \frac{2\int_0^R t_r r dr}{R^2}$$

where t_r is the thickness of the unaccommodated lens at a point r from the axis of the lens, and R is the pupillary radius under consideration. t_r in millimetres is shown in Fig. 1 and the relative values of $\bar{x}$ in Fig. 2. The scale on the left shows by what dilution factor density measurements obtained for the pupillary centre (LUDVIGH and MCCARTHY, 1938) have to be multiplied if the diameter of the experimental pupil is given by a value shown along the abscissa. Conversely the scale on the right shows the concentration factor to be applied to

density data obtained for a large pupil when the experimental pupil is small. SAID and WEALE (1959) used dilated pupils which were between 7·5 mm and 8 mm in diameter. The concentration factors on the right-hand scale are calculated on the basis of the lower value, thus providing a lower limit for the correction to be applied. The fact that pencils of light do not generally travel along paths parallel to the axis of the lens can be shown to be of little importance.

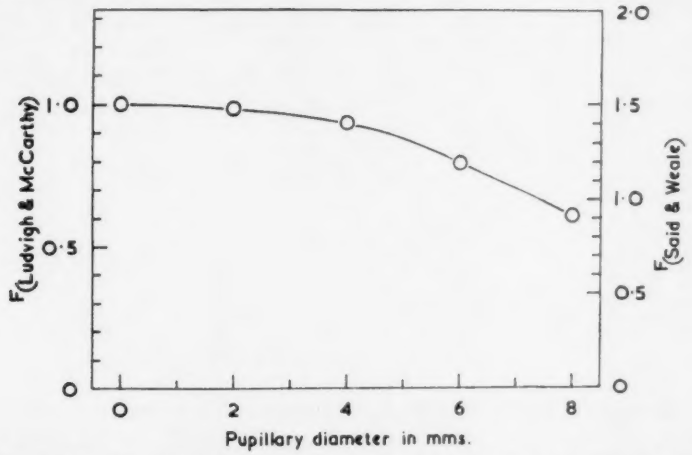

FIG. 2. The relative effective pathlength, $\bar{x}$, of the lens as a function of the pupillary diameter. Left ordinate: dilution factor for LUDVIGH and MCCARTHY's measurements; right ordinate: concentration factor for SAID and WEALE's measurements.

It follows from Fig. 2 that Ludvigh and McCarthy's results are applicable only to experimental data in conditions in which the effective entrance pupil of the eye does not exceed 4 mm in diameter. They have actually been applied to larger pupillary diameters with consequences which will be discussed below. Conversely, SAID and WEALE's (1959) original data are applicable only to results obtained with large pupils, such as CRAWFORD's (1949), and they have, in fact, been shown to be remarkably successful in connexion with some previously unexplained features of just that investigation.

3. APPLICATIONS

In the following, the above theory is applied to several problems; while it is obvious that in more than one example the data involved have been obtained on too few subjects to ensure universal applicability, they may nevertheless command attention.

(*a*) *Perimetric Fields*

The measurement of perimetric fields provides the ophthalmologist with a powerful diagnostic tool. Relatively few workers seem to have studied physiological variations of the fields, but MANN and SHAPLEY (1947) have published data giving the variation of the extent of dark-adapted fields with age (Fig. 3). Possible reasons for the contraction of the fields observed for advancing years were mentioned, but none examined. This may be due to the still prevalent view that the retina deteriorates with age (cf. PILLAT, 1952) and numerical assessment of decay is unpopular. One faces the question of whether the extent of

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the contraction may not perhaps be predicted. Let us recall in this connexion that the pre-Goldmann–Weekers perimeters as used in Great Britain are relatively crude instruments, providing a fixed physical stimulus (the variable disk size is immaterial in this connexion).

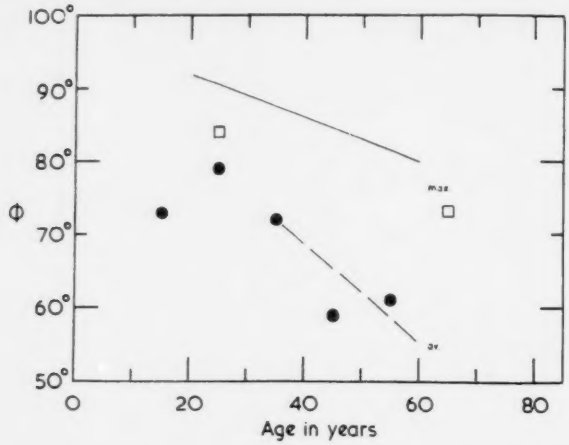

FIG. 3. Estimates for the age variation of the extent of the visual field. For details see text.

A priori, then, the retina of a subject with a small pupil will receive less light than if the pupil were large and, as the field is determined by a threshold measurement, will give rise to a different field than if the pupil were large. As, moreover, the retinal periphery is, in general, less sensitive than the more central areas, a contraction of the fields will be diagnosed. Now the dark-adapted pupil of people in their twenties admits 1·6 times as much light as that of people in their sixties (BIRREN *et al.*, 1950; KADLECOVÁ *et al.*, 1958). If the data shown in Fig. 2 are combined with the above reliable values for the age-variation of the pupil and with the data of WEALE (1954) and SAID and WEALE (1959) for the variation with age of lenticular transmission, it is possible to calculate the variation with age of retinal illumination for any illuminant, including incandescent lamps. STILES and CRAWFORD (1937) and SLOAN (1950) have published data for the sensitivity of the eye at various retinal locations. The ages of their subjects being known, it is possible to calculate what threshold values would be obtained if the physical stimulus were kept constant but the retinal illumination reduced by factors due to the pupil and lens variations. Now Mann and Shapley's indication of their stimulus intensity is not entirely unambiguous (WALSH, 1953). Furthermore they give the extent of the field in terms of an average vector which can lead to difficulties in interpretation. In face of these difficulties, one can somewhat arbitrarily consider the extremes of the meridional curves of Stiles and Crawford and of Sloan and apply the pupil and lens variations to these points (it being assumed that at low luminance levels the profile curve is not very sensitive to the level of adaptation). The resulting age variation of the average of the extreme values is shown by the dashed line (Fig. 3). The continuous line shows the contraction of the temporal side of the horizontal meridian alone and is compared with single data obtained by HAGER (1958). Uncertainty regarding the level of adaptation decreases the reliability of the latter comparison. The contraction with age of the dark-adapted field hence seems approximately accounted for by physical factors: previous writers (cf. HAGER, 1958) have, perhaps, been unduly pessimistic regarding retinal stamina.

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(b) The Absolute Threshold

This less gloomy outlook is fortified by a consideration of the age variation of the absolute threshold. For the purpose of this discussion, five investigations have been selected without bias and it so happens that the authors who controlled the pupillary size used blue

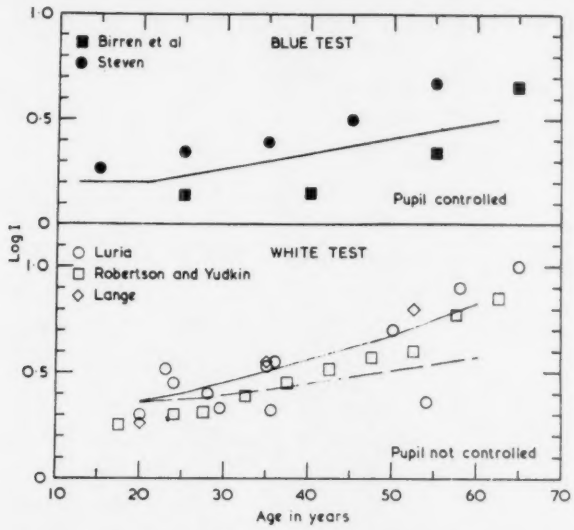

FIG. 4. Age variation of absolute threshold in relative units.

light, while those who employed a natural pupil used white. The former data (top, Fig. 4) are fairly satisfactorily described by the age variation of lenticular density (———). If the pupil correction alone is applied to the other data (bottom, Fig. 4), the agreement is less satisfactory (— — —) than when the procedure described in the previous section is adopted (———). We see once again that the age variation of physical factors can explain that of visibility fairly satisfactorily at least in the rod range.

(c) Other Estimates for Lenticular Density

STILES and BURCH (1959) have provided an interesting estimate of the variation of pre-retinal absorption as a whole and, by a judicious consideration of certain shape irregularities together with a density spectrum of the macular pigment, tentatively separated the relative contributions of the crystalline lens and the macular pigment respectively. Fig. 5 shows their estimate, on the assumption that no ageing of macular pigment occurs, together with Said and Weale's data, corrected for a very narrow pupil (STILES, 1956). The comparison for 400 mμ (where macular pigment is not believed to absorb) is excellent by any standard. It deteriorates rather markedly in the region of macular pigment absorption, but improves again at longer wavelengths. The agreement between the two sets of data could be materially improved by a suitable choice of a base line for the data of Stiles and Burch. In fact, Fig. 5 presents the comparison in the worst possible light.

(d) Comparison between the Visual Purple Absorption Spectrum and the Scotopic Spectral Visibility Curve

CRESCITELLI and DARTNALL (1953), who have made an excellent study of the properties of human visual purple, compared its absorption spectrum with CRAWFORD's V_λ curve (1949). They quantized these results and applied Ludvigh and McCarthy's data to allow for pre-retinal absorption. Crawford states: "In all measurements the full natural pupil was used. . . ." Reference to Fig. 2 in the present paper shows that an application to Crawford's

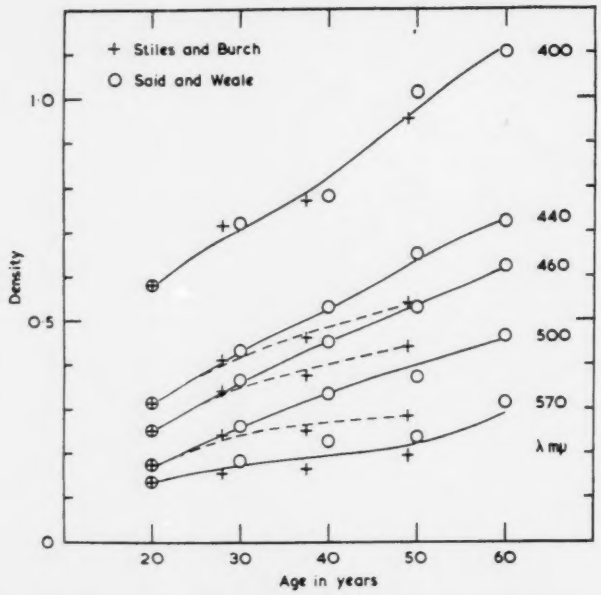

FIG. 5. Comparison of age variation of lenticular density near the pole of the lens by two different methods.

data of Ludvigh and McCarthy's values involves an over-correction. If this is allowed for, the newly corrected visibility curve is displaced by 2 mμ towards longer wavelengths. One would hesitate to ascribe any great significance to the consequent small discrepancy between the visual purple absorption spectrum and the scotopic spectral visibility curve respectively, although it may perhaps partly be due to a minute Purkinje shift contingent to Crawford's experimental conditions.

(e) The Stiles–Crawford Effect

STILES and CRAWFORD (1933) discovered that rays passing through the pupil eccentrically are visually less efficacious than those entering the eye near the centre. They considered the effect of corneal reflectivity and losses associated with the lens and, though the requisite data to enable them to allow adequately for these effects were not then available, were able to show that the effect must be retinal in nature. So far from even a small fraction of the pupillary selectivity being accounted for by differences in light losses within the eye, as stated by BRINDLEY (1960), it can be shown that, if the theoretical considerations in Section 2 above are valid, these losses counteract the selectivity. One of the ways of measuring the

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Stiles–Crawford effect is to direct at the retina two narrow pencils of light, one passing near the pupillary centre, the other at a variable distance d away from it. Equal radiances in the two pencils produce different brightnesses. These can be equated by suitable means, the resultant ratio of the two radiances η providing a measure of the effect: in general, though

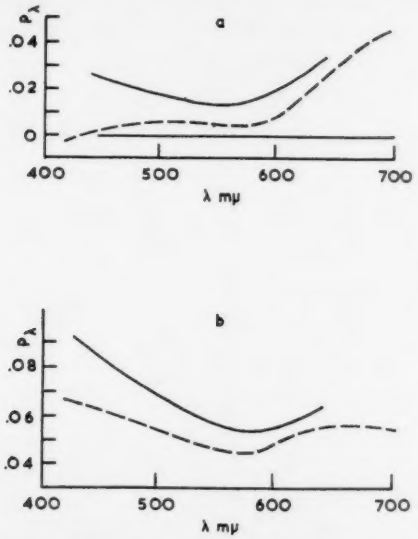

FIG. 6. (a). Spectral variation of the Stiles–Crawford effect in the parafovea (5°) before (— — —) and after (———) allowing for lens transmissivity. (b). Ditto for the fovea.

not always, the radiance of the pencil passing near the pupillary centre has to be reduced to achieve this. Clearly the pathlength of this pencil through the lens is greater than that of the other (test) beam: consequently some of the requisite reduction in radiance is being achieved by the lens. Where the effect is detected it is measured as being smaller than it would be if the lens were flat. Stiles and Crawford found that η was approximately related to d by a Gaussian function:

$$\text{Log } \eta = P_\lambda (d - d_m)^2$$

where d_m is the distance of the point from the geometrical pupillary centre for which the visual efficacy of the beam is maximal. P_λ varies with the wavelength in the manner shown in Fig. 6(a) for the dark-adapted parafovea at 5° and in Fig. 6(b) for the dark-adapted fovea. Actual measurements across the pupil are shown in Fig. 7, where log U_λ is the energy in the test-beam, related to that in the matching beam $(U_\lambda)_m$ by

$$\eta = \frac{U_\lambda}{(U_\lambda)_m}$$

The dotted lines in these figures reproduce the data obtained by STILES (1939), the continuous ones the same data when the correction for the differential lenticular pathlength has been applied (Fig. 1). Points of interest are, first, that in the fovea, the blue part of the spectrum reveals a directivity of the retina far in excess of that shown by radiations of long wavelengths when the correction is used. Secondly, the data for the parafovea can no longer be deemed to offer unequivocal evidence for the conclusion that rods have negligible

directional properties. They are smaller than those attributed to the cones, as revealed by the portion of the curve for wavelengths greater than 600 mμ (Fig. 6(b)), but not overwhelmingly so. At the moment it is not clear to what extent differences in receptor numbers may affect the situation. The observation that rods may have measurable directional properties provides another example (cf. WEALE, 1961) in support of the view that the differences between rods and cones are perhaps less circumscribed than a rigid generalization of the Duplicity Theory would allow one to believe.

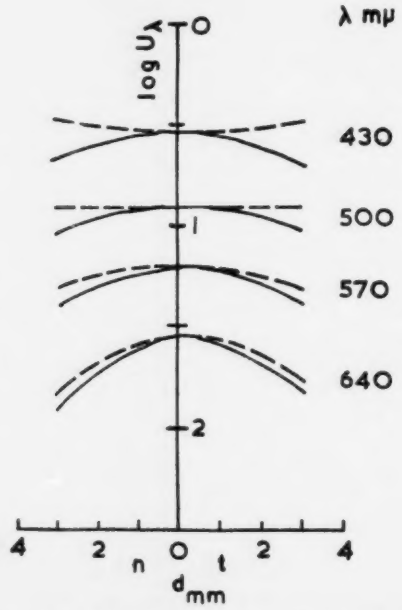

FIG. 7. Measurements of the foveal Stiles–Crawford effect for various wavelengths. For key see Fig. 6.

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THE ATTENUATION OF OPTOMOTOR RESPONSES IN WHITE-EYED MUTANTS OF *MUSCA DOMESTICA* AND OF *COELOPA FRIGIDA*

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(*Received 26 October 1960*)

Abstract—The visual acuity of white-eyed mutants of *Musca domestica*, which are entirely lacking in isolating eye pigmentation, was compared with that of wild-type flies by means of their optomotor reactions. Within a wide range of conditions and using different criteria it was found to be less than one-twelfth of the normal.

The similar white-eyed mutant "white" of the seaweed-fly *Coelopa frigida* also showed greatly reduced optomotor reactions and another mutant "sherry" hardly any such responses.

Résumé—L'acuité visuelle de mutants à yeux blancs de *Musca domestica*, dont les yeux manquent totalement de pigment isolant, est comparée au moyen des réactions optomotrices à celle de mouches de type sauvage. Dans un large domaine de conditions et avec des criteria différents, on obtient une acuité plus de douze fois moindre que la normale.

De même pour les mutants à yeux blancs de la mouche des varechs *Coelopa frigida*, les réactions optomotrices sont fortement réduites pour les mutants "blancs" et presque absentes pour d'autres mutants "ambrés".

Zusammenfassung—Die Sehschärfe des Auges einer weiss-augigen Mutanten der Hausfliege *Musca domestica* das keinerlei Färbung des Auges aufzeigte, wurde mit dem einer normalen Fliege verglichen und die optomotorischen Reaktionen beider Augen wurden gemessen. Die Auswertungen dieser Messungen wurden in einem weiten Bereich der experimentellen Verhältnisse ausfüllt und haben gezeigt das die Sehschärfe des Auges diser Mutanten um ein zwölftel tiefer liegt.

Auch die optomotorischen Messungen an einer ähnlichen, mit "weiss" bezeichneten Mutante der Seetangfliege *Coelopa frigida* haben diese Herabsetzung der Sehschärfe gezeigt, wahrend eine "Sherry" Mutante nur eine geringfügige Differenz gab.

INTRODUCTION

THE absence in eye mutants of the pigments which normally affect the optical isolation of the ommatidia in the apposition eyes of diptera might be expected to result in a loss or reduction of their visual acuity; and it has indeed been shown that white-eyed mutants and mutant combinations in several species of *Drosophila* (KALMUS, 1943) and in *Culex* (KALMUS, 1946) do not react optomotorically inside a striped rotating cylinder, while the wild types, carrying normally pigmented eyes, do; partial loss of eye pigmentation in *Drosophila* is accompanied by some loss in optomotor performance (KALMUS, 1943).

These results, while demonstrating the rôle of pigmentary isolation, did not provide a basis for a quantitative estimate of its efficiency. Such an opportunity, however, arose when a white-eyed mutant of the housefly which was given to the author turned out to be entirely lacking in eye pigments and yet, quite contrary to expectation, showed distinct if attenuated

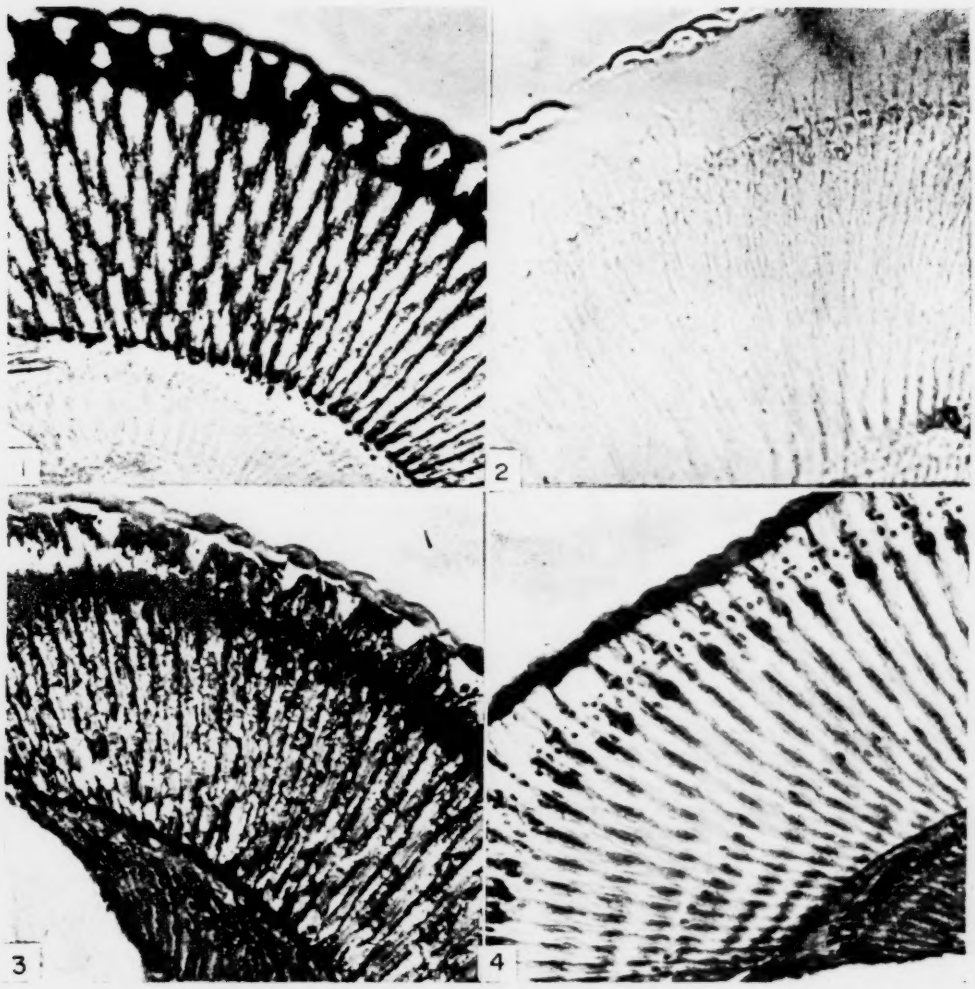

FIG. 1. Sections through the eyes of *Musca domestica* (300×). Left, wild type; right, white homozygote; top, unstained; bottom, Ehrlich's *haemat. eosin*. Photograph: Dr. Frances Molloy. (Left, showing the primary pigment surrounding the pseudocones, the basal pigment and the secondary pigment in cells surrounding the retinula cells.)

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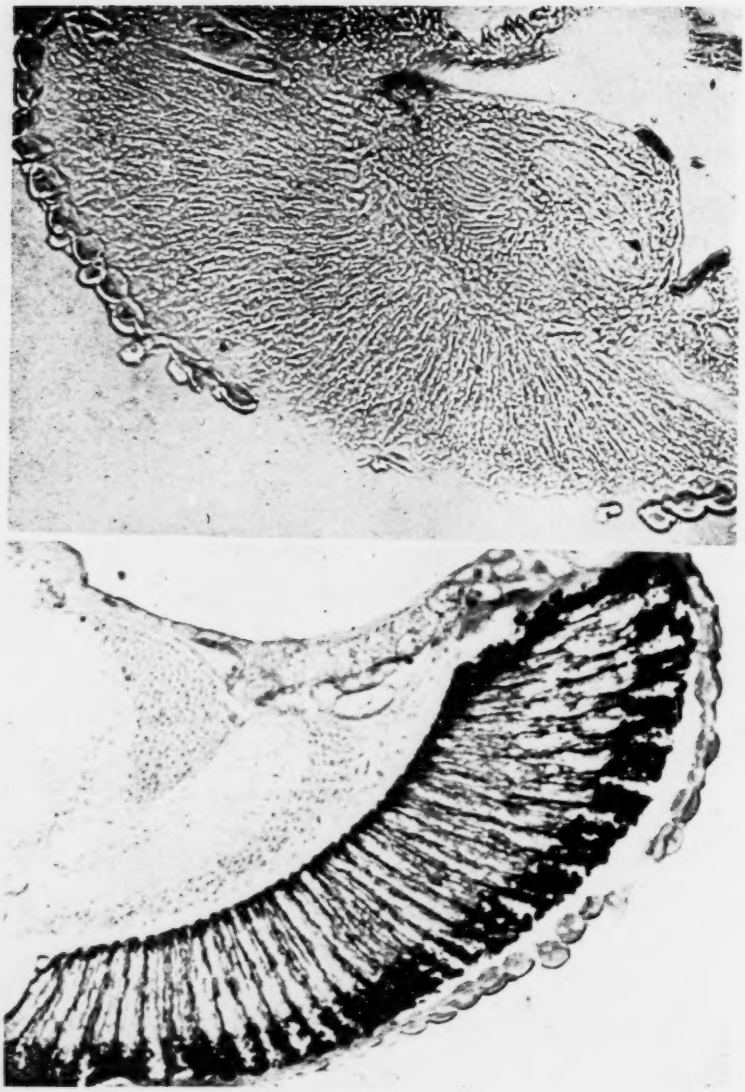

FIG. 2. Sections through the eyes of *Coelopa frigida* (400×). Top, wild type showing primary, basal and secondary pigment; bottom, "sherry" showing lack of pigments. Unstained. Photograph: Dr. Frances Molloy.

reactions in the rotating striped cylinder.[1] Two eye mutants of a somewhat smaller fly, the seaweed-fly *Coelopa frigida*, were also used for comparison.

MATERIAL

Light-eyed individuals[2] were observed in an inbred strain of *Musca domestica* in the Department of Insecticides and Fungicides of Rothamsted Experimental Station, Harpenden. The condition was shown to be autosomal recessive by the usual breeding procedures. Histological examination revealed no pigment in the "white" eyes of $\frac{w}{w}$ flies reared at 28°C. The eyes of the heterozygotes were pigmented (Fig. 1) and no difference in pigmentation could be detected between these and the wild-type homozygotes; nor was any difference in the optomotor reactions of the two genotypes demonstrable. All the same, in most experiments $\frac{w}{w}$ and $\frac{w}{+}$ back, cross segregants of the same age and sex and from the same cultures were used for comparison. Three cultures of the seaweed-fly *Coelopa frigida* were obtained from the Department of Zoology, King's College, Newcastle-upon-Tyne, namely a wild type and two recessive eye mutants, "white" and "sherry", entirely lacking in eye pigments (Fig. 2). No crossings were made and individuals from the original cultures were used in the experiments.

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FIG. 3. Maze for scoring optomotor reactions. Diameter 7 cm.

APPARATUS

The apparatus for testing optomotor reactions has been previously described in detail (KALMUS, 1943 and 1946); it consists mainly of two horizontal circular platforms which are coaxially mounted and can be turned independently. On the smaller and higher platform can be put various types of containers or holders, while the larger lower disk supports exchangeable striped cardboard cylinders, and can be turned and reversed either by hand or

[1] Prof. H. Autrum has observed optomotor reactions in white-eyed *Caliphora erythrocephala*, while confirming my finding of their absence in white-eyed *Drosophila*; I am grateful for his permission to mention these findings.

[2] The eye colour of the newly emerged mutant flies was quite white, that of older flies light brown; wild-type *M. domestica* has dark red eyes.

by a small motor. Light is provided by an opal incandescent bulb of 40 W suspended 60 cm above the flies.

Ideally insects should be tethered to provide a constant visual situation and their reactions observed by the effects of their feet on a mobile object (HASSENSTEIN, 1958), but houseflies react rather erratically under such conditions. On the other hand unfettered flies must be prevented from escaping and then the necessary constraints interfere with the reactions.

Two different arrangements using freely running flies proved fairly satisfactory; one consisted of an inverted watch-glass of 5 cm diameter, which rested on a piece of cardboard, on which was drawn a radius, the crossing or recrossing of which by the fly was scored. This arrangement is very sensitive and faint patterns were sufficient to induce and to measure optomotor reactions. The other arrangement (Fig. 3) consisted of a simple maze cut from black perspex sheets offering a running fly four dichotomies and covered by a transparent disk. This arrangement was less sensitive and strong visual patterns had to be used with it. Scoring methods for both arrangements are described together with the result.

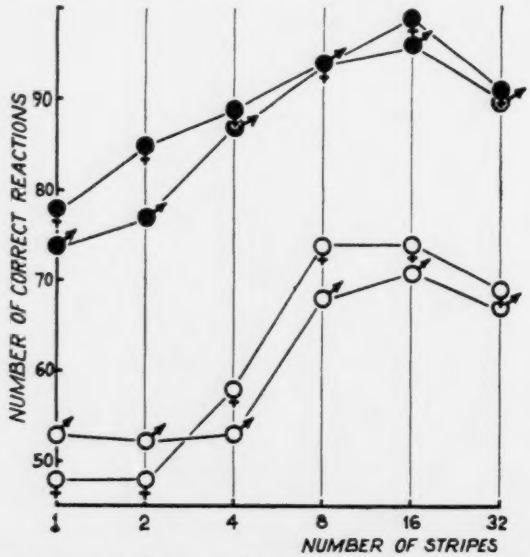

FIG. 4. Positive passages out of 100 of wild-type and white-eyed *Musca domestica* during continuous periods of clockwise (50 passages) and counterclockwise (50 passages) pattern movements (1 r.p.s.). Reflectancies as measured with an Evans Electroselenium spectro-photometer—white areas: 78·5 per cent in the blue, filter 601; 82·0 per cent in the green, filter 605; 87·0 per cent in the extreme red, filter 609—grey areas: 73·5 per cent blue; 78·5 per cent green; 83·5 per cent extreme red (T = 28 °C).

RESULTS

Fig. 4 shows results of experiments using the watch-glass arrangement. The rotating cylinders, 20 cm high and 20 cm in diameter, were made from white Bristol board of about 80 per cent reflectancy as compared with magnesium carbonate, carrying varying numbers of 4 mm wide vertical light grey stripes of about 75 per cent reflectancy.

It appears that (1) the sixteen-stripe pattern had the strongest effect on all flies, (2) that the wild-type individuals reacted quite strongly throughout the range tested, while (3) the white-eyed flies showed no response below four stripes and (4) were less responsive to all patterns.

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Fig. 5 shows results obtained by the use of the same kinds of flies in the *Y* maze and using much stronger visual patterns as well as a different scoring method. The black stripes on the Bristol board cylinders were of about 5·5 per cent reflectancy, 5·5 per cent in blue and green, 6 per cent in extreme red and of equal width to the alternating white stripes.

In these experiments the maximum efficiency was observed with patterns of twelve stripes while otherwise the absolute and relative responses were rather similar to those summarized in Fig. 4.

A different scoring method was employed in experiments combining the watch-glass arrangement with the strong visual patterns employed in Fig. 5 and measuring reversal times with a stop-watch (Fig. 6).

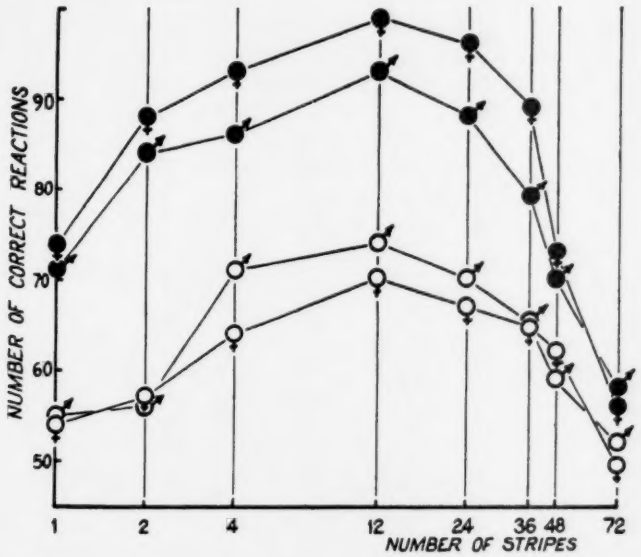

FIG. 5. Positive turns at bifurcations and on the spot, of wild-type and white-eyed *M. domestica* during clockwise and counterclockwise pattern movements, each continued for 50 turns (T = 28°C).

TABLE 1

Pattern	3 black stripes 12·5 mm wide			3 light grey stripes 2·5 mm wide			12 equal black-and-white stripes		
r.p.s.	1/2	1	2	1/2	1	2	1/2	1	2
Wild type ...	93	97	99	74	83	91	95	98	98
"White"	49	52	57	49	52	55	63	63	54
"Sherry" ...	52	52	48	53	50	50	56	52	53

Number of correct passages out of 50 during clockwise and 50 during counter-clockwise pattern movement of females of *Coelopa frigida* homozygous for wild type, "white", and "sherry" (T = 25°C).

The results obtained with the seaweed-fly *Coelopa frigida* were less regular and are summarized in Table 1. It shows that the wild type shows marked optomotor reactions while those of the mutant white are greatly attenuated and those of the mutant sherry almost non-existent.

DISCUSSION

Optomotor reactions are based on an integrative utilization of the successive stimulation of the visual elements (KALMUS, 1949) and in particular on multiplicative interactions of neighbouring and nearby ommatidia (HASSENSTEIN, 1958). These interactions depend on the optical isolation between the ommatidia and a numerical assessment of the effect which this pigmentary isolation has on visual acuity can be based on a comparison of patterns which will evoke equally strong optomotor reactions in pigmented and unpigmented eyes. Figs. 4 and 5 show that in a wide range of conditions and using different criteria houseflies with normal eyes are at least twelve times as efficient as white-eyed flies. This estimate is

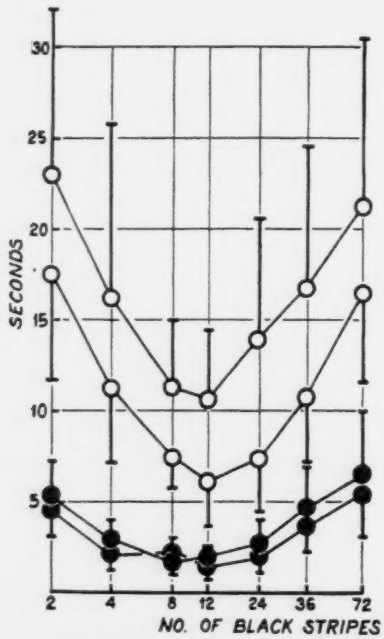

FIG. 6. Average reversal times of male *M. domestica* after 20 reversals of striped cylinders. ● wild-type, ○ white-eyed flies, top 2 r.p.s., bottom 1 r.p.s. (T=28°C).

based on measurements near the most accurate level of responses, namely 75 per cent positive responses, which is half-way between a fifty–fifty result (no response) and total success. It can be seen that in both figures the best responses of the white-eyed flies (those to patterns of twelve and sixteen stripes) barely reach 75 per cent, while the results of the wild-type flies to one stripe are in the same neighbourhood. Similarly the shortest reversal time achieved by the white-eyed flies in Fig. 6 occurred when the twelve-stripe pattern revolved twice every second, which is still longer than the reversal time of normal flies to but two stripes. A more sophisticated consideration of the effects of pigmentation on visual

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acuity would have to take into account that, *ceteris paribus*, less light reaches the photosensitive stratum in the pigmented eye than in the unpigmented eye; that some of the patterns differ in overall brightness; that the photokinetic effect of twelve stripes does not in most circumstances equal exactly twelve times the effect of a single stripe (KALMUS, 1949). This and other considerations would render a more accurate estimate of little value.

It might be asked, at this point, why the reduction in optomotor responses, by the lack of isolating eye pigment, should differ so markedly in various diptera, as pointed out in the introduction. One reason might be the difference in absolute eye size, which results in a greater facet number and thus increased visual acuity and sensitivity (BARLOW, 1952) in the larger *Musca* and *Coelopa* as contrasted with the smaller *Drosophila*. Lack of isolating pigmentation would then only reduce the resolving power of the larger eyes, but abolish it altogether in the smaller eye. While this is probably true, it cannot be the whole explanation and in particular it cannot explain why the attenuation of optomotor responses should differ between the mutants "white" and "sherry" in *Coelopa frigida*, the eyes of both of which appear equally depigmented.

Acknowledgements—I want to thank Dr. FRANCES MOLLOY, of Rothamsted Experimental Station, for preparing and photographing the sections of eyes, Miss T. KRUGGEL, also of Rothamsted, for keeping the stocks of *M. domestica* and Dr. B. BURNET of the Zoology Department of King's College, Newcastle-on-Tyne, for the stocks of *Coelopa frigida*.

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EDITOR'S NOTES

COMMANDER DEAN FARNSWORTH, to whom this first issue is dedicated, was Scientific Liaison Officer with the Office of Naval Research in London at the time of the earliest conception of *Vision Research*. His rôle was critical in establishing publisher contact, and in soliciting much of the widespread cooperation which our international advisory board now reveals. *Vision Research* would not have been possible without him.

Several friends and colleagues have joined in this present memorial, that his inspiration may be perpetuated.

* * *

The closest precursor to *Vision Research* is, perhaps, the great *Zeitschrift für Psychologie und Physiologie der Sinnesorgane*, founded officially on 10 February 1891 by Hermann Ebbinghaus and Arthur König. In close association with them were: H. Aubert, S. Exner, H.v. Helmholtz, E. Hering, J.v. Kries, Th. Lipps, G. E. Müller, W. Preyer and C. Stumpf. Certainly much of the development of visual science was in the hands of these men, though by no means all. The *Zeitschrift* split in 1907, into the *Z. f. Sinnesphysiol.*, edited by W. A. Nagel and the *Z. f. Psychol.*, edited by H. Ebbinghaus.

But these journals did not survive World War II.

Further, there is a gap more important than time between these journals and *Vision Research*. The present Journal reflects a division of the senses, not of the sciences. Physiology, chemistry, neurology, zoology, morphology, physics, psychology, mathematics—in short, all branches of knowledge concentrate here on a common problem. Increasingly convinced of the value of the inter-disciplinary approach, we find ourselves relying more and more on theories and hard facts supplied by colleagues with whom our predecessors seldom spoke. Dual photopigments, for example, do not prove the existence of qualitative color experience; narrow electrophysiological peaks do not prove the existence of narrow photopigments; psychophysical discontinuities do not prove the duplexity theory. The fact of accommodation does not disclose its mechanism; nor does the existence of structures disclose their function. There is hardly a theory worthy of the name today in visual science which does not need to seek support from traditionally adjacent fields.

* * *

The spirit of scientific internationalism is growing. It is hoped that *Vision Research* will continue to serve this end, as have the recent international congresses out of which most support for *Vision Research* has come.

"Visual Problems of Colour",
National Physical Laboratory,
Teddington, England.
23–25 September 1957.

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"Photoreception",
The New York Academy of Sciences,
New York City, U.S.A.
31 January and 1 February 1958.

"Mechanisms of Colour Discrimination",
Collège de France,
Paris, France.
25–29 July 1958.

Vision Research will try to carry announcements and reports of similar congresses whenever they occur and would like at this time to call attention to the following:

"Symposium über die Physiologie des visuellen Systems",
Freiburg im Breisgau,
Germany.
28 August–3 September 1960.

Whenever such conferences are planned in the future, the Editors would be pleased to have advance notice of them so that they may be listed here.

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* * *

On the eighth day of June 1637 a book appeared, from Leyden, Holland, written in the French language, which marked in a singular way the commencement of the modern visual science of man. It included one of the earliest correct and elegant illustrations of the formation of the retinal image in man. The name of the book is:

"*Methode pour bien raison.*
Discours de la methode pour bien conduire sa raison et chercher la verité dans les sciences.
Plus: La dioptrique, les meteores, et la geometrie.
Qui sont des essais de cete methode" [*sic*]

The name of the author is not given! A second Latin edition, however, soon appeared in Amsterdam, in 1644, entitled:

Specimina Philosophiæ sev Dissertatio de Methodo, recté regendæ rationis, et veritatis in scientiis investigendæ:
Dioptrice et Meteora. Ex Gallico translata, et ab Auctore prelecta, variisque in locus emendata.

The author's name appears here: Renati Des Cartes.

It is from the first French edition (1637) of René Des Cartes' (*b.* 31 March 1596–† 11 February 1650) *La dioptrique* that our cover picture is taken. It appeared in this edition no less than seven times (pp. 37, 39, 42, 45, 61, 76, 116) and—possibly slightly touched up, judging from small differences in lines and shading—nine times in the Latin edition (pp. 100, 103, 105, 107, 109, 111, 125, 138, 172).

Des Cartes was illustrating Scheiner's experiment (1625) wherein the sclera and choroid were removed from the fundus of the eye of an ox and the image was observed from behind, on a white piece of paper or an egg-shell.

However, there is much more to this illustration than its correct description of the inversion of the retinal image, for the observer himself appears in a singular rôle. Perspective, at this time, was well enough advanced so that the eye being drawn twice as large as the head of the observer had to have been drawn deliberately. This is certainly partly to display the "ray-tracing" inside the eye to its best advantage.

I would like to suggest that implied in this severe violation of perspective is a more profound idea of Des Cartes' which he here leaves unsaid, though only in this context. For Des Cartes, the pineal gland, that singular organelle at the base of the brain, was the point of intersection of the mind and the body, of spirit and matter. It was at this point that the soul of man could be localized. It was from here that the inner homunculus peered out through the sensory portholes.

Hence, the drawing is not only a description of Scheiner's experiment, it is also a description of man observing his own retinal image, of the mind's eye taking stock of the external reality. The fact that Des Cartes used this picture over and over again—he used only one other (in explanation of water refraction) in a similar fashion—suggests that it may have meant more to him than just an illustration.

The mythopoeic conception of the inner eye, the *Ultimate Cyclops*, is one of the archetypes of mankind; it recurs throughout ancient and medieval history and in almost all primitive societies known to us today. It has, and always will have, associations of power, fear, mystery, evil masculinity, and intangibility. It probably had these meanings no less for Des Cartes than for his contemporaries.

In this image of self-observation, Des Cartes also implicitly embodied an explanation of the origin of experimental science, as emerging from the introspective regard for sensory experiences. It was Galileo, at this very same time, who made the step explicit. From an arm moving, a man walking, a ball rolling, so Galileo turned to moving or motion in and by itself.

In Des Cartes' illustration we have a man observing himself seeing; we may even have a second man, deviously, observing the first man seeing. We have an implicit observation of seeing in and by itself.

Nihil in intellectu est quod non antea fuerit
in sensu, nisi intellectus ipse. . . .

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ON ACQUIRED DEFICIENCY OF COLOUR VISION,* WITH SPECIAL REFERENCE TO ITS DETECTION AND CLASSIFICATION BY MEANS OF THE TESTS OF FARNSWORTH

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(*Received 17 October 1960*)

Abstract—Some three-quarters of a century ago the various forms of acquired colour vision deficiencies had already been well studied by Koenig, von Kries, Koellner, and other German scientists using spectral devices. However, these studies have been greatly neglected, and it is only within the last few years that there has been a renewed interest in this field, of which the first approach has been greatly facilitated in the meantime by the Panel D-15 and the 100-Hue of FARNSWORTH. Generally speaking, nearly all ocular diseases give rise to absorption systems, while lesions in the deeper layers of the retina elicit a predominant reduction of the blue–yellow sense, and lesions in the ganglion layer and in the optic nerve mainly result in a reduction of the red–green sense.

Résumé—Il y a environ soixante-quinze ans, les différentes formes de dyschromatopsie acquise furent fort bien étudiées, à l'aide des méthodes spectrales, par Koenig, von Kries, Koellner, et d'autres chercheurs allemands. Ces données furent négligées par la suite et ce n'est que depuis quelques années qu'il y a un renouveau d'intérêt dans ce domaine, dont le premier abord a été entretemps facilité par l'emploi des tests Panel D-15 et 100-Hue de FARNSWORTH. D'une façon générale, toutes les affections oculaires donnent lieu à des systèmes d'absorption; les lésions des couches profondes de la rétine sont surtout accompagnées par une réduction de la discrimination du bleu et du jaune, tandis que les lésions de la couche des cellules ganglionnaires et du nerf optique affectent surtout la discrimination du vert et du rouge.

Zusammenfassung—Vor ungefähr fünf und siebzig Jahren, wurden die erworbenen Farbenfehlsichtigkeiten, vermittels der Spektralmethoden, von Koenig, von Kries, Koellner, und anderen deutschen Forscher eingehend studiert. Angaben wurden später nicht mehr beachtet; seit einigen Jahren entstand erst neues Interesse an diese Forschungsgebiet, das man nun bequemer angehen kann weil die Teste Panel D-15 und 100-Hue von FARNSWORTH zur Verfügung stehen. Meistens erzeugen alle Augenkrankheiten Absorptionssysteme; die Läsionen der tiefen Lagen der Netzhaut sind sehr oft begleitet von einer Herabsetzung des Blau–Gelb-Unterscheidungsvermögens, während Läsionen der Ganglienzellschicht und des Nervus opticus vor allem das Unterscheidungsvermögen für Grün und Rot betrifft.

IT IS obvious that the development of the knowledge of the acquired colour vision defects has been greatly retarded in comparison with that of the congenital ones.

Nevertheless, it must be emphasized that both major classes of colour vision deficiency have been actively studied at the end of the nineteenth and the beginning of the twentieth century. This is the great period in which Helmholtz and other German scientists made the first precise colorimetric investigations of human vision.

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* *Editor's note*—This paper was originally scheduled for the inaugural issue; because of its particular relevance to the theme of that issue the Editors are sorry that structural matters have delayed its appearance. The authors especially wished to add their names to the memorial for Commander Dean Farnsworth, and we hope that through this note this wish may adequately be made known.

For example, one can find in Helmholtz's *Physiological Optics* an extensive colorimetric study of the colour vision defect which is elicited by the ingestion of santonin. However, it was Koenig who discovered the most important basic facts. In a case of tobacco intoxication, he described an acquired red–green blindness, wherein the cold curve was identical to that of the protanope and of the deuteranope, whilst the warm curve was intermediary to that proper to these two kinds of congenital red–green blindness. Furthermore, he showed in 1897 that the mixture curves in a case of retinal detachment are identical to those of a congenital tritanope and he also found "acquired tritanopias" in subjects suffering from hypertensive retinitis. In the same year, 1897, von Kries established the important distinction between the congenital alteration system and the acquired absorption system. Further important concepts have been discussed by Nagel, Simon and others. All these facts have been very well summarized and classified by Koellner and by Hembold.

After this "German period", the study of colour vision was pursued principally by Anglo-Saxon physicists and physiologists; since then, whilst our knowledge of normal vision and of the typical congenital defects was becoming remarkably accurate, the acquired defects were so neglected that the facts already known were almost completely forgotten and eventually cases of acquired deficiency were even considered as congenital.

Indeed, even today, acquired colour blindness is often considered to be rare, because it is not recognized as such; in fact, it is very frequent since, generally speaking, it is present as soon as visual acuity is reduced by any pathological process whatsoever in the retina or in the optic nerve.

Of course, this negative evolution is due not only to the fact that the ocular diseases are properly recognized only in ophthalmological clinics, but also because the acquired deficiencies are rather intractable owing to their heterogeneity and are complicated by concomitant impairment of other visual functions.

Now, the use of the tests of FARNSWORTH has encouraged a new approach to the study of the acquired deficiencies in an unhoped-for way. But, before referring to the actual use of these tests, perhaps it is useful to emphasize the differences which exist between the congenital forms of colour vision deficiency and the acquired ones.

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DIFFERENCES BETWEEN CONGENITAL AND ACQUIRED DYSCHROMATOPSIAS

The main differences can be itemized as follows—

(a) The severity of the acquired defect can increase or decrease as long as the responsible pathological lesion is evolutive.

(b) The acquired defect is often localized in one eye or even in a part of one eye.

(c) The acquired defect can vary in severity or can be different in different parts of the affected area; the defect often becomes less pronounced when the apparent size, the luminance or the exposure time of the test field is increased.

(d) The acquired defect generally occurs together with an impairment of other visual functions such as visual acuity, dark-adaptation and flicker-discrimination.

(e) The recently affected subjects name the stimuli as they see them. This is in contrast to the congenital or long-established acquired defects, where there is then no secondary adaptation of their colour naming to that of normal trichromates.

(f) All contrast phenomena are generally reduced in subjects with acquired defects. However, the contrast between colours, which are still recognized, is normal or even seemingly increased in the congenital anomalous trichromatic and dichromatic systems. (Some pseudo-isochromatic plates, which the normal trichromate cannot read, are based on this principle.)

(g) The acquired defects are very often made manifest as absorption systems, but perhaps never as alteration systems.

(h) The acquired defects are very often reduction systems, but the condition can evolve so that it does not remain a reduction system.

(i) In the acquired reduction systems, the remaining hue-discrimination is generally worse than that in the corresponding congenital defect.

(j) The confusion axes eventually acquired can have different distributions and/or different directions from the congenital ones.

(k) The acquired defects are often characterized by chromatopsia.

The items (g)–(k) need some explanation.

Ad (g)—The "absorption system" and the "alteration system" have been defined by VON KRIES (1897). Their distinction is of foremost importance in the comparative study of the acquired and congenital colour vision defects.

The absorption system is the result of a pre-receptoral selective absorption. It can be produced in the laboratory by placing a colour filter in front of the examined eye; in pathology, it is produced by nearly all conditions which affect the transmissive properties of the ocular refringent media. When this condition exists some normal colour matches are no longer accepted. Furthermore, when mixtures of two monochromatic lights of constant wavelengths λ_a and λ_b are matched successively against monochromatic lights $\lambda_1, \lambda_2, \lambda_3 \ldots$ and when the proportions of λ_a to λ_b required by the subject to match $\lambda_1, \lambda_2, \lambda_3 \ldots$ are plotted against those required by a normal subject, then one finds that the quotient of anomaly (that is, the ratio of the abnormal to normal proportions) remains constant. This, of course, is due to the fact that the ratio of the abnormal pre-receptoral absorptions of λ_a and λ_b itself remains constant.

The alteration system is encountered in the congenital anomalous trichromatic systems. Here also some normal colour matches are not accepted. But when mixtures of the lights of constant wavelengths λ_a and λ_b are matched against the monochromatic lights $\lambda_1, \lambda_2, \lambda_3 \ldots$ and when the required proportions of λ_a and λ_b are plotted against those required by a normal subject, then one finds that the quotient of anomaly does not remain constant. It is possible to demonstrate that this is due to the fact that one of the three fundamental response curves of the anomalous trichromate is altered in such a way that it cannot be reproduced by a linear combination of the three normal response curves.

Of course, an abnormality of the luminosity curve may be expected in an absorption system as well as in an alteration system.

Now, an isolated or concomitant absorption system is extremely frequent in the acquired deficiencies, whilst it never functions as the cause in the congenital case; on the other hand, a true alteration system is probably never acquired, whilst it is the cardinal feature of the congenital anomalous trichromatic systems.

Ad (h)—The "reduction system" is usually defined as a sensory condition in which hue-discrimination is a two-fold function instead of a three-fold function of the wavelength and in which all matches of a normal trichromate are accepted. It is easy to demonstrate that there are then only two fundamental response curves and that they can only be linear combinations of the three normal ones; accordingly, a reduction system can only be realized either by the loss of one of the normal fundamentals (Helmholtz–Koenig mechanism), or by the collapse of two normal fundamentals (Leber–Fick mechanism). Theoretically, the luminosity curve can be entirely normal in some varieties of the Leber–Fick mechanism.

A broader definition of the reduction system includes not only dichromatic conditions, but also some acquired trichromatic and monochromatic ones; furthermore, the cases with abnormal pre-receptoral transmission are no longer discarded. The following requirements must still necessarily be met: (1) the hue-discrimination must be worse than in a normal trichromate; (2) all matches of a normal trichromate, the eye of whom is fitted with a convenient filter, must be accepted.

The two principal kinds of acquired colour vision deficiency, namely acquired red–green blindness and acquired blue–yellow blindness, are always reduction systems in this enlarged sense. Each of these two conditions can proceed from normal trichromatism through an abnormal trichromatic stage (which is a reduction system and not an alteration system) towards a dichromatic stage and further to a monochromatic stage, and then to complete blindness; the stage at which the impairment of normal vision stops, and from which it may recover, depends on the causal pathological lesion. However, it does happen, in extreme stages, that the photopic mechanisms are so damaged that the scotopic ones predominate even in photopic circumstances; the normal photopic matches are then no longer accepted and the condition is no longer a reduction system.

Ad (i)—In acquired red–green blindness and in acquired blue–yellow blindness, the hue-discrimination, of course, is mainly affected in the direction of one axis of the normal chromaticity chart, though a concomitant impairment of the hue-discrimination in the direction at right angles to this axis also occurs. If this concomitant impairment is absent or weak, however, as soon the vision has become dichromatic, the acquired defect closely resembles a congenital dichromatism; on the contrary, if this concomitant impairment

is strong then the acquired defect more closely resembles first a colour amblyopia and then later some kind of congenital atypical achromasy. It is always this concomitant impairment which leads the acquired deficiency from the dichromatic stage to the monochromatic one.

Ad (j)—In both types of acquired dichromatic reduction systems, the main neutral axis, which can be plotted in the normal chromaticity chart, has a much greater range of dispersion in direction than in a congenital dichromatic system. In some instances, it is even difficult to ascertain if the subject is affected by a red–green blindness or by blue–yellow blindness, because the neutral axis is found right in the middle between that of congenital deuteranopia and that of congenital tritanopia. Furthermore, it is impossible to identify acquired red–green blindness with protanopia or deuteranopia, or acquired blue–yellow blindness with tritanopia or tetartanopia, because the range of the neutral axes widely overlap those of the two corresponding congenital conditions. (However, this statement must not be considered as an argument in favour of the polychromatic theories, because this variability can easily be explained, namely by the conjunction of the reduction system with an absorption system.)

Ad (k)—Chromatopsia may be defined as a condition in which stimuli, being white for the normal trichromate, appear to be coloured. Various chromatopsias have occasionally been described in each of the ocular diseases. These can be due either to a quickly formed absorption system or to a temporary imbalance in the physiological mechanisms at the retinal or at the cerebral level. Although the phenomenon is very obvious, generally it can be correlated to the colorimetric findings only with difficulty. Chromatopsia is always a temporary condition, since the definition of the various colours does adapt to a new equilibrium. This is characterized by the fact that stimuli which are white, for the normal, are again labelled as such.

N.B. The recognition defects, which are characteristic of the pathological conditions affecting the highest levels of the optic pathways, will not be studied in this paper. A typical symptom of this group is the inability to name any colour, although the colorimetric performances are those of a normal trichromate.

METHODS OF EXAMINATION

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During the period which preceded the editing of our monograph (FRANÇOIS and VERRIEST, 1957b), we used the pseudo-isochromatic plates of Ishihara and Polack, the Tritan Plate, the Panel D-15 and the 100-Hue of Farnsworth, the anomaloscope of Nagel, the colour naming of twelve selected monochromatic stimuli (method of Koellner), the calibration of the spectral regions 530–640 mμ and 470–510 mμ by means of the colorimeter of Helmholtz, the method of Walls and Mathews for the study of the entoptic perception of the macula, perimetry with coloured objects by means of the perimeter of Goldmann, and the study of the electroretinograms elicited by neon light flashes. We later added the pseudo-isochromatic plates of Hardy, Rand and Rittler and also the study of the photopic luminosity curve by means of both the flicker and the direct matching methods.

After examining the findings we came to the conclusion that it is always necessary to utilize several tests in order to obtain a secure diagnosis. It is often beneficial to examine the eye with the poorest vision first.

1. *For the Recognition of the Type and Extent of an Acquired Reduction of Colour Vision*

For this only the Panel D-15, the 100-Hue and the colour naming of spectral stimuli are very useful.

Indeed, the pseudo-isochromatic plates, which are intended for the detection of the congenital colour vision defects, are often unreliable, owing to the concomitant impairments of hue-discrimination and to the great range of dispersion in the direction of the confusion axes. However, the plates of Hardy, Rand and Rittler are often useful. OHTA (1957c) has made special plates for the acquired defects, but we have no experience of them.

The Panel D-15 enables us to make the diagnosis even in cases in which the visual acuity, the visual field, and the colour discrimination itself are very poor, but the mild cases escape; on the contrary, the 100-Hue detects these mild cases, but the tracings soon become uninterpretable as the disease progresses. On the other hand, the Panel can be administered to children as young as four or five years, whilst the tedious 100-Hue is rarely performed

correctly by observers under ten years. Of course, fully standardized lighting, such as is given by the Macbeth Executive Daylight Lamp, is necessary in order to run the tests of Farnsworth, and also all the other pigmentary tests, under convenient and reproducible experimental conditions. Retest is often useful.

The twelve wavelengths, which we selected for the application of the method of Koellner, are the following: 435, 471, 490, 495, 507, 535, 551, 575, 589, 610, 656, and 690 mμ. They were obtained by means of the colorimeter of Helmholtz.

The subject, afflicted by the dichromatic stage of an acquired red–green blindness, behaves as a deuteranope when tested with the anomaloscope. This instrument does allow one to compute the general shape of the luminosity curve in the different forms of red–green blindness and in achromasy, but, of course, it is better to study the curve with greater accuracy.

2. *For the Recognition of an Absorption System*

For this the anomaloscope is a convenient test. However, certain proof that we are dealing with an absorption system can only be obtained by means of the colorimeter and calculation of the quotient of anomaly for various wavelengths. Chromatopsia is diagnosed when a small piece of white paper is given a colour attribute by the subject.

3. *For the Differential Diagnosis Between Acquired and Congenital Colour Vision Defects*

For this it is more than ever necessary to use different tests. The subjects affected by congenital anomalous trichromatism display an (apparently) increased colour contrast when tested with the anomaloscope. This symptom is absent in all acquired defects. All subjects affected by congenital anomalous trichromatism or dichromatism do read certain pseudo-isochromatic plates, which are not recognized by the normal trichromates. The subjects with acquired colour blindness do not read these plates. Finally, congenital defects can also frequently be distinguished from the acquired ones by the fact that they generally affect the whole visual field of both eyes, e.g. in congenital protanopia and in congenital typical achromasy, the red test of the Goldmann-perimeter is not seen anywhere in the visual field and the global electroretinographic responses to neon light flashes are characterized by an apparent lack of the photopic b_1-wave.

NOTE ON THE DEVELOPMENT OF THE USE OF THE TESTS OF FARNSWORTH IN THE STUDY OF ACQUIRED DYSCHROMATOPSIAS

JAEGER (1956a) wrote that, in acquired cases of defective colour vision, there will always be an alteration of the visual acuity and colorimetric measurements will most often be quite impossible. Thus it seemed necessary either to seek out types of acquired colour deficiency which had a visual acuity sufficient to obtain some colour mixture data or to modify our colour tests, so that persons with reduced visual acuity might also be examined. In fact the Panel D-15 and the 100-Hue have fulfilled the last requirement perfectly, with regard to the detection and the classification of the acquired reduction of colour vision.

Nevertheless, the 100-Hue was first used, in this field, for the recognition of an absorption system, namely by JUDD, PLAZA and FARNSWORTH (1950).

STEINMETZ, OGLE and RUCKER (1956) were the first to utilize the 100-Hue for the recognition of an acquired colour blindness. They found by means of this test and of the Hardy–Rand–Rittler pseudo-isochromatic plates, that the blue–yellow discrimination was particularly affected in some cases of degeneration of the deeper macular layers.

Independently of them, we gave prominent significance to the results obtained by means of the Panel D-15 and of the 100-Hue in our studies on acquired colour vision deficiency (FRANÇOIS and VERRIEST, 1956,

1957a, 1957b, 1958, 1959; FRANÇOIS, VERRIEST and DE ROUCK, 1956, 1957; FRANÇOIS J., VERRIEST, FRANÇOIS P. and ASSEMAN, 1961). In our monograph (FRANÇOIS and VERRIEST, 1957b) we have already referred to the examination of some 150 subjects by these methods. OHTA (1957a–d) made exhaustive studies on the colour sense in fifteen cases of retinitis pigmentosa by means of the 100-Hue and other devices. BOZZONI (1959) has studied 138 cases of various eye diseases by means of the Panel D-15 and of the 100-Hue, and COX (1959) has examined about 150 cases by means of the 100-Hue and other devices including Wright's colorimeter. Meanwhile some isolated observations have been made by several authors, namely Goodman, Dubois-Poulsen, Zanen, Perdriel and others.

CLASSIFICATION AND PRACTICAL RECOGNITION OF THE VARIOUS TYPES OF ACQUIRED DYSCHROMATOPSIA

After the lengthy explanations in the previous paragraphs, it is very easy to define and to outline the symptoms of the different types of acquired colour vision deficiency.

1. *A (Pure) Absorption System*

This is obtained when the selective absorption of the pre-receptoral structures exceeds the normal range. It can touch every part of the visible spectrum in a selective manner. Chromatopsia is present when the modification of the spectral transmittance is recent, and important.

The study of the colour naming shows that the colours corresponding to the most highly absorbed wavelengths are darkened; the colour which is complementary to the hue of the eventual chromatopsia appears less saturated than it does for a normal subject. The luminosity curve is necessarily altered. At the anomaloscope, Rayleigh's match is generally clearly abnormal, while the colorimeter allows us to obtain the very typical results which have been described above (i.e. the quotient of anomaly is constant). The readings of the pseudo-isochromatic plates and the arrangements of the Panel D-15 and of the 100-Hue are normal in mild cases. However, the inter-relations with the other forms of acquired defective colour vision are very important and complex.

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2. *The Acquired Blue–Yellow Deficiency*

In this or Hong's "retinal group" of acquired colour sense disturbances—one can distinguish a trichromatic stage and a dichromatic stage.

(*a*) *The trichromatic stage of the acquired blue–yellow deficiency*. This is a trichromatic reduction system, which is always associated with an absorption system and frequently associated with a faint concomitant red–green defect. Some of the synonyms referring to this condition are: acquired tritanomaly, Collin and Nagel's violet-anomaly and Simon's "erworbene Violettblindheit im physikalischen Sinne".

The study of the colour naming shows that confusions occur in the "cold corner" of the normal chromaticity chart. These apply to some purple, violet, blue, and green hues. The hue-discrimination is normal elsewhere and there is no neutral zone.

At the anomaloscope, Rayleigh's match is normal or slightly displaced towards the protanomalous side; the colorimeter shows that this pseudo-protanomaly behaves as an absorption system. The third law of Grassmann is no longer upheld.

The reading of the usual pseudo-isochromatic plates is not characteristic; however, it is important to note that the figures, which are not recognized by the normals, are also not read in this condition. The Panel D-15 tracings are generally characterized by numerous errors from cap 11 to cap 15, but, in some instances, the arrangement of the caps 1–7 is also disturbed and even diametral tritan-confusions can appear. The 100-Hue gives a very

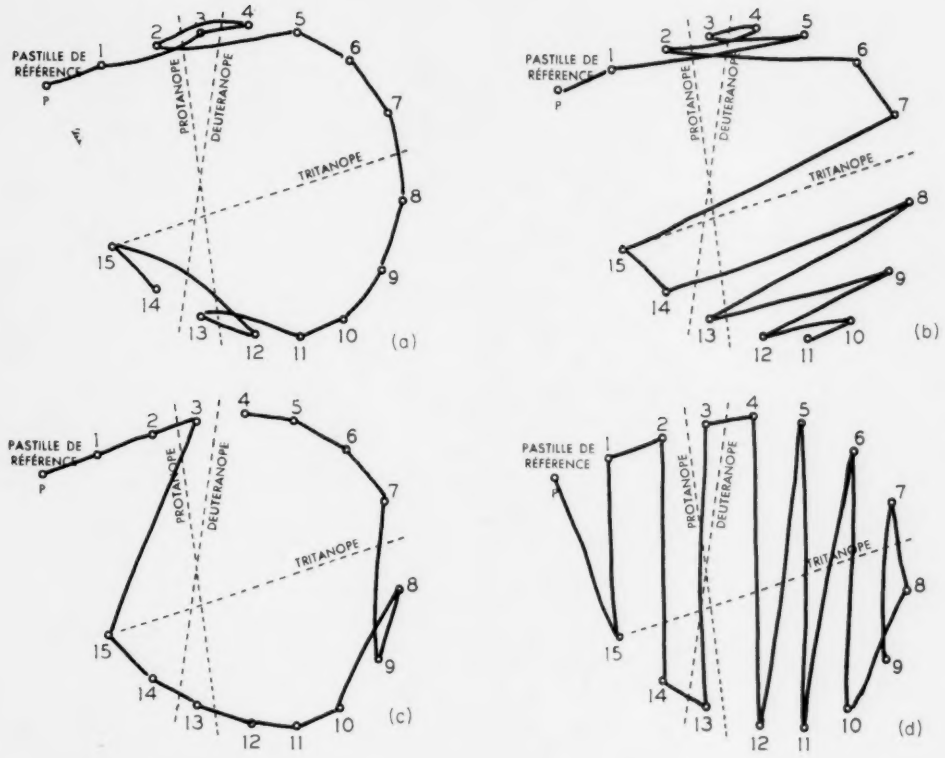

FIG. 1. Panel D-15. Typical tracings for:

(*a*) the trichromatic stage of acquired blue–yellow blindness (from a case of macular choroidal sclerosis);

(*b*) the dichromatic stage of acquired blue–yellow blindness (from a case of retinitis pigmentosa);

(*c*) the trichromatic stage of acquired red–green blindness (from a case of juvenile macular degeneration);

(*d*) the dichromatic stage of acquired red–green blindness (from a case of retrobulbar neuritis).

characteristic monopolar bulge of which the centre corresponds to the caps 48–58. Farnsworth's Tritan Plate does not permit the diagnosis of this defect.

(*b*) *The dichromatic stage of the acquired blue–yellow deficiency.* This is a dichromatic reduction system, which is always associated with an absorption system and with a concomitant red–green defect. Some of the synonyms referring to this condition are: acquired tritanopia, acquired blue-blindness, Helmholtz's acquired violet-blindness and Simon's "erworbene Violettblindheit im physiologischen Sinne".

The study of the colour naming shows that there is an obvious neutral zone between 550 and 580 mμ and another neutral zone around 465 mμ. The violet, blue, and blue-green tints are considered as colourless, blue or green, the green ones as green (except 520–550 mμ which is often very typically labelled as blue), the yellow ones as colourless, rose, red, purple, or blue, the orange and red ones as red. It was formerly claimed that the visible spectrum is shortened at the short-wave end; however, the recent measures show that it is the luminosity

FIG. 2. 100-Hue. Typical tracings for:
(*a*) the trichromatic stage of acquired blue–yellow blindness (from a case of closed-angle glaucoma–monopolar tracing).

of the long-wave half which is particularly depressed in severe cases (HONG, 1957; COX, 1960; *pers. ob.*).

At the anomaloscope, Rayleigh's match is nearly always widened and displaced towards the protanomalous side; the colorimeter shows that this pseudo-protanomaly behaves as an absorption system. Grassmann's third law is not upheld (HONG, 1955).

The reading of the usual pseudo-isochromatic plates is not any more specific here than in the trichromatic stage. The tracings of the Panel D-15 are of the dichromatic type, the mean axis being either the typical tritan one or an axis shifted clockwise or counter-clockwise. The 100-Hue is of the bipolar tritan, tetartan or deutan/tritan type. According to COX (1959), most of the cases of "acquired tritanopia" give a vertical axis with the 100-Hue test, corresponding to Farnsworth's original plotting for tritanopia (which he

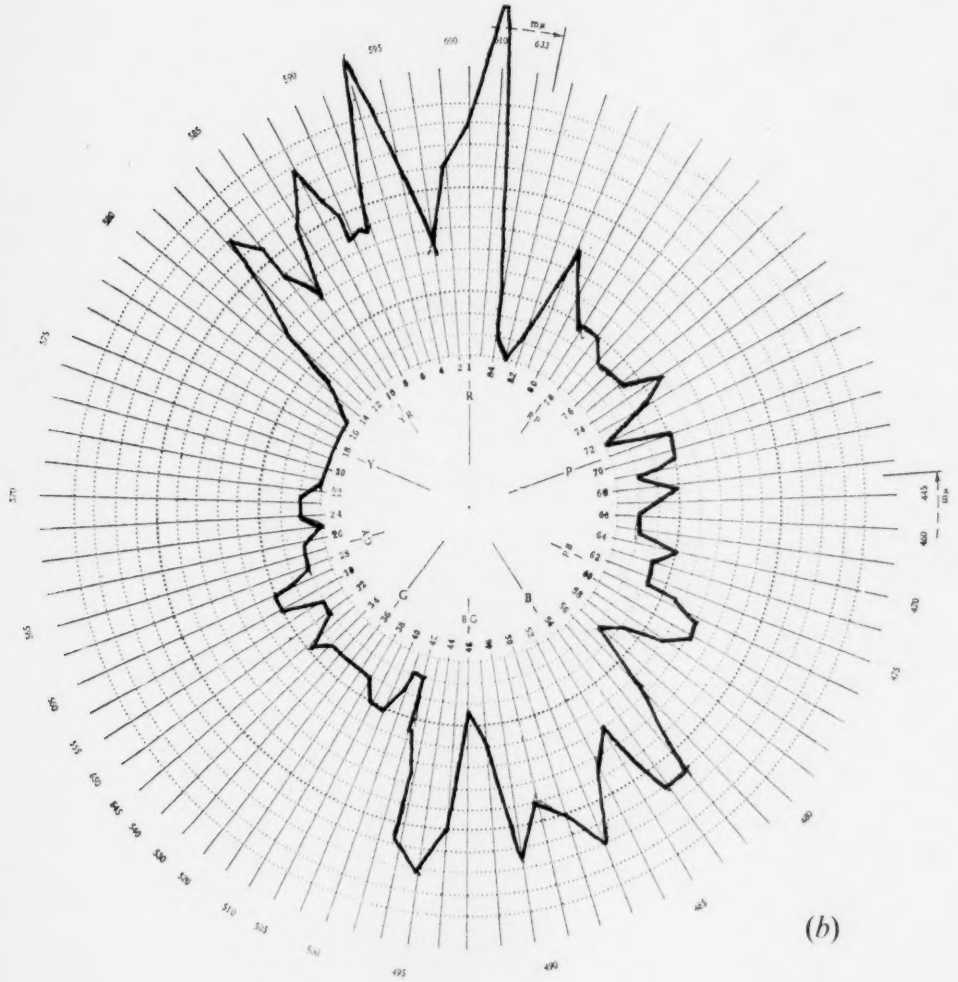

FIG. 2. 100-Hue. Typical tracings for:
(*b*) the dichromatic stage of acquired blue–yellow blindness (from a case of retinitis pigmentosa).

thought to be influenced by an absorption system due to an incipient cataract). However, BOZZONI (1959) has computed a different mean axis for each retinal disease. The Tritan Plate does not often permit diagnosis of this defect.

The concomitant damage of the red–green sense can lead to achromasy. The blue–yellow defects are generally associated with a great impairment of the dark-adaptation range.

3. *The Acquired Red–Green Deficiency*

In this or "progressive Rot–Grünblindheit", Engelking's "progressive konkomittierende Farbensinnsstörung", and Hong's "neural group" of acquired colour sense disturbances, one can also distinguish a trichromatic stage and a dichromatic stage.

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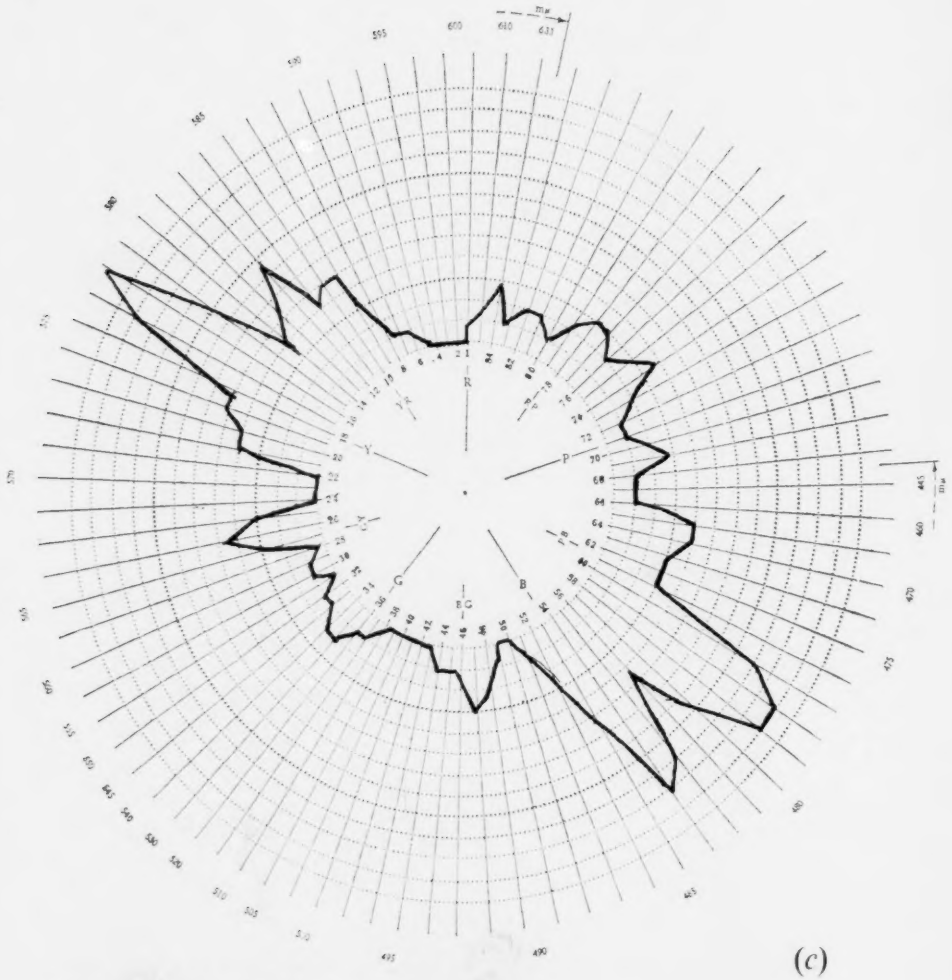

FIG. 2. 100-Hue. Typical tracings for:
(*c*) the trichromatic stage of acquired red–green blindness (from a case of tabetic optic atrophy).

(*a*) *The trichromatic stage of the acquired red–green deficiency.* This is a trichromatic reduction system, which is nearly always associated with an absorption system and a concomitant blue–yellow defect.

The study of the colour naming shows that there is no neutral zone, although the saturation is often diminished in all spectral and non-spectral regions. The violet tints are considered as violet or blue, the blue ones as blue, the greenish-blue ones as pale blue, the bluish-green ones as pale green, the green–yellow ones as pale yellow, the yellow ones as yellow, the orange ones as yellowish, the red ones as red and later as orange.

At the anomaloscope, Rayleigh's match is always widened and generally displaced towards the deuteranomalous side; the colorimeter shows that this pseudo-deuteranomaly behaves as an absorption system. The third law of Grassmann is upheld.

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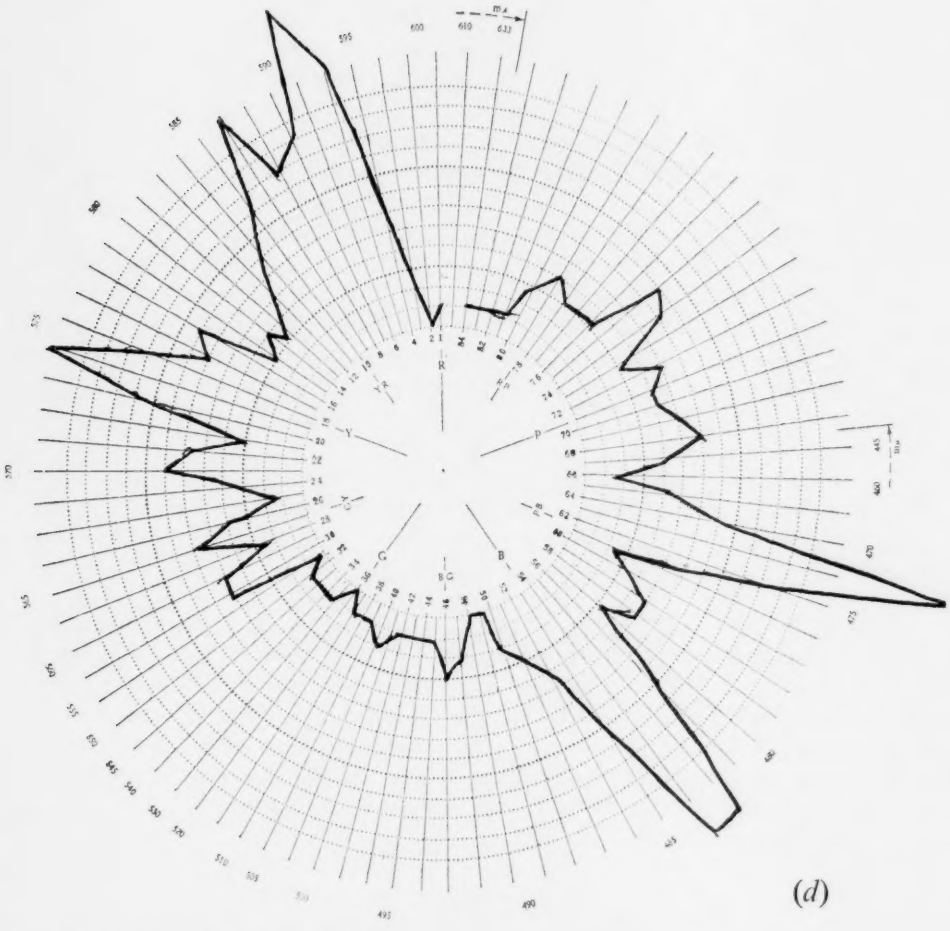

FIG. 2. 100-Hue. Typical tracings for:

(*d*) the dichromatic stage of acquired red–green blindness (from a case of Leber's hereditary optic atrophy).

The affected subject is often unable to read either the pseudo-isochromatic plates which are not recognized by the deutan subjects or those which are not recognized by the normals. The Panel D-15 tracings are characterized by some protan or deutan confusions, which are often accompanied by many minor errors. The 100-Hue gives a high score. The tracing resembles that of a congenital colour amblyopia, or that of a congenital deutan type.

(*b*) *The dichromatic stage of the acquired red–green deficiency.* This is a dichromatic reduction system, which is nearly always accompanied by a concomitant blue–yellow defect.

The study of the colour naming shows that there is a neutral zone in the blue–green spectral region; it is first located at 490–500 mμ, but rapidly becomes very large owing to the concomitant blue–yellow defect. The second neutral zone is found in the vicinity of the boundary between the red and the non-spectral reddish-purple. The violet tints are considered as violet or blue, the blue-green ones as colourless, the bluish-green, the green and the yellowish-green ones as pale yellow, the yellow and orange ones as yellow, the red ones

also as yellow, or as colourless (neutral zone), or as red (secondary adaptation). It was formerly claimed that the luminosity curve always remains normal, but recent measures show that it is sometimes greatly shifted towards the short wavelengths, especially in Leber's hereditary optic atrophy (COX, 1960; *pers. ob.*).

However, at the anomaloscope, the affected subject generally behaves as a congenital deuteranope, with this difference: that the (luminosity) matches between the yellow and the red and between the yellow and the green stimuli are somewhat widened. The normal Rayleigh match is accepted. The third law of Grassmann is upheld.

All pseudo-isochromatic plates, which are intended to be read in congenital red–green defects, are often unreadable, as well as the plates which are not read by the normals. The tracings of the Panel D-15 are of the dichromatic type, the most frequent mean axis being right in the middle between the congenital protan axis and the congenital deutan axis; criss-crossings may occur (concomitant blue–yellow defect). The 100-Hue is either of the deutan type or wholly anarchic. The blue square of the Tritan Plate is not visible, as in congenital red–green blindness.

(*c*) *A special kind of acquired red–green deficiency*. This is encountered in cases of juvenile macular degeneration and is characterized by the fact that the normal match of Rayleigh soon ceases to be acceptable and, accordingly, the condition no longer remains a reduction system (see below in the analytic section).

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4. *Acquired Total Colour Blindness*

This can be the final result of many conditions: the combination of a congenital protanopia with an acquired blue–yellow blindness; the combination of a congenital deuteranopia with an acquired blue–yellow blindness; an acquired blue–yellow blindness which has evolved towards achromasy owing to the concomitant red–green defect; an acquired red–green blindness which has evolved towards achromasy owing the concomitant blue–yellow defect; and the special kind of red–green deficiency which has evolved towards achromasy by the impairment of all photopic mechanisms.

OCCURRENCE OF THE ACQUIRED COLOUR VISION DEFICIENCIES IN THE VARIOUS OCULAR DISEASES

In principle, all *pathological modifications of the transparency of the pre-retinal refringent media* give rise to absorption systems. For example, the shorter wavelengths are obscured in jaundice (SEKI, 1954) and in incipient cataract (OBI, 1954; FRANÇOIS and VERRIEST, 1957b). Albinism can be classified in the category of the absorption systems, as the discrimination is normal whilst the luminosity curve is shifted towards the longer wavelengths, which is due to an increased reflexion of the light by the choroidal blood vessels (DODT, COPENHAVER and GUNKEL, 1959).

A transient chromatopsia is often an obvious sign of the establishment of an absorption system. Examples are the cyanopsia after a cataract extraction and the erythropsia after a pre-retinal extravasation of blood.

The *peripheral choroido-retinal degenerations*, of which retinitis pigmentosa is the most current variety, are characterized by an acquired blue–yellow blindness with a long-lasting dichromatic stage. This has been known for a long time and has recently been extensively re-stated by ourselves (FRANÇOIS, VERRIEST and DE ROUCK, 1956; FRANÇOIS and VERRIEST, 1956; 1957b), OHTA (1957a), BOZZONI (1959) and COX (1960). In 1956 and 1957, we had the impression that the colour vision defect was rather precocious, as we dis-

covered it in twelve out of seventeen subjects. However, this statement was not in accordance with that of KOELLNER (1906), who found a normal colour sense in sixteen out of twenty-three subjects; with that of LEBER (1916), who showed that the macular colour vision remains normal as long as the visual acuity is not affected, nor is it in accord with that of GOODMAN and GUNKEL (1958), who found no acquired defects in some cases of rather benign retinitis pigmentosa with dominant mode of inheritance; with that of SMITH, RIPPS and GOODMAN (1959), who also found no acquired defects in cases of retinitis punctata albescens; with that of ZANEN (1959), nor finally with that of COX (1960) who found normal colour vision in nine out of sixteen patients. Our material has now increased to a total of forty-five subjects, of which thirty-one have a blue–yellow defect, three an indefinite defect, and eleven normal colour vision or only congenital defects. We also found entirely normal vision in four women who are heterozygotes for sex-linked retinitis pigmentosa or choroideremia.

With regard to the luminosity curve, HESS (ref. LEBER, 1916) and LARSEN (1923) showed that the values for the short wavelengths are lower than in the normal and that there is a shift of the maximum ordinate of the curve towards the long wavelengths. We have so far examined three cases (with the flicker method) and, in one of these cases, we have found not only that the values for the short wavelengths are diminished, but also that the long-wave half is even more depressed than in protanopia.

On the other hand, it is well known that subjects affected by retinitis pigmentosa match as protanomals when tested with the anomaloscope. By means of the Helmholtz colorimeter, we have shown that the quotient of anomaly remains constant when the wavelength of comparison is altered. The condition is thus similar to an absorption system. FARNSWORTH (1959) has interpreted the clockwise shift of the 100-Hue axis in some of our first cases of acquired blue–yellow blindness in retinal degenerations as due to an abnormal retinal pigmentation.

OHTA (1957a–d) showed that the evolution of the disease can be subdivided into three stages, as far as colour vision is concerned: in the first stage, Rayleigh's match is still normal and the 100-Hue appears defective only at low illuminations; in the second stage, Rayleigh's match is displaced towards the protanomalous side and the 100-Hue is of the tritan type even in the usual experimental conditions; in the third stage, the equalization zone at the anomaloscope can be greatly enlarged towards the deuteranomalous side and the 100-Hue tracings can become anarchic. Normal colour vision in the small central field is similar to that of this acquired tritanopic condition.

Subjects of congenital protan or deutan defects together with retinitis pigmentosa are very liable to develop total colour blindness, as the acquired defect progressively impairs the remaining blue–yellow discrimination (survey of the literature: FRANÇOIS, VERRIEST and DE ROUCK, 1955).

It has been known for a long time that *juvenile degeneration of the macula* can be accompanied by three types of acquired colour blindness: (a) a blue–yellow blindness, (b) a red–green blindness and (c) a total colour blindness. Furthermore, there are also cases where the colour vision is normal, as all visual functions: SORSBY and WREN (1960), *pers. obs.*

Recent observations on the (a)-eventuality are those of LANDOLT (1955), STEINMETZ, OGLE and RUCKER (1956), HONG (1957), BOZZONI (1959) and COX (1960); it is generally obvious that these cases refer to degenerations of the deeper layers of the macula, as shown by the pigmentary disturbances. We have also observed such cases, but we are inclined to consider them as atypical forms of retinitis pigmentosa.

The (b)-eventuality has been described by SORSBY and DAVEY (1955), FRANÇOIS and VERRIEST (1956, 1957b) and COX (1960). It refers mainly to subjects in which the macular region shows no abnormal pigmentation, but only a viscous appearance and many white dots. In some cases of this particular kind of degeneration, the acquired colour vision defect more closely resembles congenital protanopia, as the luminosity curve is depressed in the long-wave half (true congenital protanopia being excluded because the peripheral colour vision is normal). In some further cases of the same affection, we observed a (c)-eventuality: the macular region here is then characterized by a total colour blindness with a photopic luminosity curve which may be considered as identical to the normal scotopic one (FRANÇOIS, VERRIEST, DE ROUCK and HUMBLET, 1956). JAEGER (1956b) and COX (1960) have studied similar cases, where the juvenile macular degeneration was also thus associated with a luminosity curve shifted towards the normal scotopic function. We are inclined to conclude that this apigmentary type of juvenile macular degeneration is characterized by a progressive alteration of both the colour sense and luminosity function, so that the affected patient should successively display a classical acquired red–green defect, a pseudo-protanopia and finally a pseudo-typical achromasy. It is necessary to emphasize that the arrangement of the Panel D-15 can remain normal, even in the last stage, merely because the patient uses his peripheral field of vision.

The (c)-eventuality, namely total colour blindness, can be due to circumstances other than the one just described: of course, it can be the result of a progressive blue–yellow defect, principally when the subject is congenitally colour deficient. It must also be remembered that congenital typical achromasy is very often accompanied by a macular dystrophy, so often, in fact, that some authors have even falsely concluded that the colour vision defect of congenital typical achromasy is due only to the macular condition.

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We have now collected fifteen cases of juvenile macular degeneration (the atypical retinitis pigmentosa being excluded): two of them have approximately normal colour vision, one has an acquired blue–yellow defect, nine have acquired red–green defects, and three have incomplete or complete acquired achromasy.

The *senile macular degenerations* are characterized by an acquired blue–yellow defect (FRANÇOIS and VERRIEST, 1957b; BOZZONI, 1959 and COX, 1960). The exudative and haemorrhagic Junius–Kuhnt-type affects the colour discrimination to a greater extent than does the more usual atrophic type. We have studied fourteen subjects, of whom three had normal colour vision, nine had an acquired blue–yellow defect, and two had an indefinite disturbance. We have observed a very typical acquired blue–yellow defect in a case of retinal *siderosis* (FRANÇOIS and VERRIEST, 1957b). The lesions of the eyeground, which are due to *myopia gravis*, also give rise to a blue–yellow defect (FRANÇOIS and VERRIEST, 1957b; BOZZONI, 1959 and COX, 1960). The quotient of anomaly can already be protanomalous even when the hue-discrimination is still entirely normal (FRANÇOIS and VERRIEST, 1957b). Our series now includes fourteen cases, of which six have a blue–yellow defect, and eight have normal colour vision or a protanomalous quotient as a single abnormality.

The acquired blue–yellow defect, which is often found in *retinal detachment*, was discovered as early as 1877 by Leber and has subsequently been carefully described by KOENIG (1897), SIMON (1905), and KOELLNER (1907b). The last-mentioned author found a trichromatic stage in six cases and a dichromatic one in twenty-six cases, the total number of subjects examined being thirty-six; he has shown that the visible spectrum is shortened at the short-wave end and that the macular colour vision disturbance is not correlated with the extent of the peripheral perimetric defects. The comparison of the affected eyes

with the contralateral ones, and the comparison of the idiopathic detachments with the traumatic ones, has shown us that the blue–yellow defect, which is found in this disease, is merely due to the pre-existing myopia gravis (FRANÇOIS and VERRIEST, 1957b). COX (1960) has reported an atypical blue–yellow defect.

Choroidoretinitis gives absorption systems and blue–yellow defects: this has been put in evidence by both the older works (e.g. KOENIG, 1897; SIMON, 1905) and the newer ones (HONG, 1957; FRANÇOIS and VERRIEST, 1957b; BOZZONI, 1959; ZANEN, 1959; COX, 1960 and PERDRIEL, 1960b). We observed the blue–yellow defect above all in active lesions and in heavily pigmented cicatricial lesions. The colour sense is normal, as are all other visual functions, in the pseudo-retinitis which is one of the ocular symptoms of the rubella-embryopathy.

COLLIN and NAGEL (1907) showed that *oedema of the macula* gives a blue–yellow defect. The particular type, which is called by ophthalmologists *choroidoretinitis centralis serosa*, has been especially well studied, namely by MORI (1916); OGUCHI (1922, 1934); DUBOIS-POULSEN (1948, 1952); JAEGER and NOVER (1951); OBI (1952); JAEGER (1955); HONG (1957); FRANÇOIS and VERRIEST (1957b); ZANEN (1959); COX (1960) and PERDRIEL (1960b). Jaeger reported that the absorption system of the longer wavelengths, which is associated with the blue–yellow blindness, should be reversible, being somewhat proportional to the amount of exudate. However, we found an absorption system as the single residual colorimetric symptom in one subject with cicatricial lesions. In a newer case, in which the colorimeter also showed an absorption system in the long wavelengths, the 100-Hue was particularly interesting because the axis of the acquired dichromatic system was accordingly greatly shifted counter-clockwise in respect of congenital tritanopia. COX (1960) also observed red–green blindness in one of three cases of central retinitis. We have studied, in all, six cases of the disease: four of them showed both the absorption system and the blue–yellow defect, and two showed only the absorption system.

The blue–yellow defect, which is due to *hypertensive retinitis*, was first mentioned by MAUTHNER (1881) and has since been carefully described by SIMON (1894, 1905); KOENIG (1897); COLLIN and NAGEL (1907); KOELLNER (1907a, 1908); HONG (1957); BOZZONI (1959) and COX (1960). The modification of the colour sense is generally confined to the macular region. We found that it only appears in the latter stages of the affliction, namely stages III and IV of the classification of Wagener and Keith (FRANÇOIS and VERRIEST, 1957b).

Diabetic retinitis also gives rise to a blue–yellow defect (SIMON, 1905; LEBER, 1916; DUBOIS-POULSEN and COCHET, 1954; HONG, 1957; FRANÇOIS and VERRIEST, 1957b; ZANEN, 1959; COX, 1960 and PERDRIEL, 1960b). Dubois-Poulsen and ourselves have shown that alteration of the colour sense is extremely frequent and that it can even precede the ophthalmoscopic signs of the disease.

The *occlusion of retinal vessels* also gives rise to a blue–yellow defect (FRANÇOIS and VERRIEST, 1957b; BOZZONI, 1959 and COX, 1960).

The older assessments relating to *glaucoma* are very inconsistent. The newer ones unequivocally demonstrate that the typical defect is a blue–yellow one (FRANÇOIS, VERRIEST and DE ROUCK, 1957; FRANÇOIS and VERRIEST, 1957b and 1959; BOZZONI, 1959 and COX, 1960). Our material can be subdivided in thirty cases of wide-angle glaucoma, of which nineteen showed a blue–yellow defect and one a red–green defect, thirty-three cases of closed-angle glaucoma, of which twenty-five showed a blue–yellow defect and one a red–green defect, and eight cases of secondary glaucoma, of which four showed a blue–

yellow defect. According to COX (1959) discrimination is often normal even when the tension is very high, and tritanopia only appears in about a third of the cases.

A *choked disk* gives rise to a blue–yellow defect (FRANÇOIS and VERRIEST, 1957b; BOZZONI, 1959), whilst *papillitis* and secondary optic atrophy give either a blue–yellow defect or a red–green one (probably according to the retinal or neural origin of the macular visual defect: HEMBOLD, 1932). We found a blue–yellow defect in one of four cases of *drusen of the optic nervehead* (FRANÇOIS and VERRIEST, 1958).

Retrobulbar optic neuritis is a condition in which the (often reversible) reduction of colour vision from normal trichromatism to achromasy and blindness is generally mediated by a trichromatic and later by a dichromatic red–green defect (KOENIG, 1897; NAGEL, 1905; MORI, 1916; VERREY, 1926; HONG, 1957; FRANÇOIS and VERRIEST, 1957b; LYNN, 1959 and COX, 1960). This is so when the condition is due to multilocular sclerosis (although ZANEN and MEUNIER (1958) and BOZZONI (1959) have at times discovered a tritan defect, namely in cases with barely reduced visual acuity), to syphilis (HONG, 1957), to tobacco–alcohol intoxication (KOENIG, 1897; VERREY, 1926; we and PERDRIEL, 1960b, have observed, rather, a colour amblyopia without prominent axis), to malnutrition, to lead or carbon sulphide-intoxication, or to diabetes mellitus (ROENNE, 1913).

Optic atrophy also is a condition in which the reduction of colour vision from normal trichromatism to achromasy is mediated by the stages of an acquired red–green blindness, the process here being irreversible. This has been stated in many cases by Koellner, HONG (1957), BOZZONI (1959) and COX (1960) among others. The older works refer principally to tabetic atrophy, which was very frequent in those days. We have found the red–green defect in cases which are attributable to traumatic or tumoral compression of the pre-genicular optic pathways, to tabes, to rimifon-intoxication, to heredo-ataxic disease, and to Leber's acute variety of hereditary optic atrophy (FRANÇOIS and VERRIEST, 1957b; FRANÇOIS J., VERRIEST, FRANÇOIS P. and ASSEMAN, 1961). It must be emphasized that the other important variety of hereditary optic atrophy, namely the infantile optic atrophy with dominant mode of inheritance, is still characterized by a blue–yellow defect (JAEGER, 1954; JOSEPH and DAVEY, 1958; KJER, 1959; FRANÇOIS J., VERRIEST, FRANÇOIS P. and ASSEMAN, 1961 and COX, 1960); the results obtained by Kok-Van Alphen are seemingly not consistent with the other ones, but it must be emphasized that this author used solely pseudo-isochromatic plates. Methyl alcohol poisoning can also give rise to a blue–yellow defect (JAEGER, 1955). ZANEN (1959) reported a tritan defect in one case of traumatic optic atrophy.

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SOME PHYSIO-PATHOLOGICAL CONSIDERATIONS

Koellner formulated a "law" according to which the lesions in the outer layers of the retina give rise to a blue–yellow defect, whilst the lesions in the inner layers of the retina and in the optic nerve give rise to a red–green defect.

That law has been greatly substantiated by the researches in the last years, which have shown that blue–yellow defects occur in retinitis pigmentosa, senile macular degeneration, siderosis retinae, myopia gravis, choroido-retinitis, and vascular occlusions, the histo-pathological picture of all these diseases being effectively characterized by a selective damage to the deeper layers of the retina; on the other hand, red–green defects do, in fact, occur in most kinds of disease of the optic nerve and of the remaining pre-genicular section of the optic pathways.

Accordingly, the study of the colour sense is very useful in the ophthalmological practice, and the convenient Panel D-15 can help the oculist in many difficult differential diagnoses. For example, when the vision of an eye of a middle-aged patient is only slightly reduced owing to the presence of a round relative central scotoma, and when the corresponding macular region shows only non-pathognomic lesions as a few white spots, the distinction between senile macular degeneration, retrobulbar neuritis and amblyopia ex anopsia is often very difficult. However, the answer is given by a study of the colour sense, as the first disease is characterized by a blue–yellow defect, the second one by a red–green defect, and the third one by normal colour vision.

With regard to ophthalmological research, the study of the acquired colour vision deficiencies is interesting, because the type of the defect is an indication of the major site of the pathological lesions in those cases wherein the histological changes are unknown or indistinct. A few examples: the blue–yellow defect in dominantly inherited optic atrophy or in glaucoma suggests a liability to involvement of the deeper layers of the macular region, and the red–green defect in some cases of juvenile macular degeneration suggests a preponderant damage to the ganglion layer.

Finally, concerning the visual physiology, the study of the acquired colour vision deficiencies is also interesting, because it completes the information given by the congenital deficiencies. No acceptable explanations have as yet been proposed to explain why retinal lesions damage the blue–yellow discrimination whilst optic nerve lesions interfere primarily with the red–green sense; nor have any been proposed to explain why the lesions of the optic nerve are characterized by an abnormal Rayleigh's match. However, with respect to the blue–yellow defect in retinal lesions, it seems to us probable that even an acquired dichromatic reduction system could eventually be due simply to a very extensive absorption of the short wavelengths, absorption which would thus exclude the relatively insensitive "blue" mechanism at the pre-receptoral level (VERRIEST, 1960).

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EINIGE ERKRANKUNGEN DES SEHNERVEN IN ELEKTRORETINOGRAPHISCHER SICHT

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Zusammenfassung—Unter Berücksichtigung der Literatur wird über klinische elektroretinographische Befunde bei einigen Erkrankungen des Sehnerven berichtet. Auch bei retinalen Atrophien braucht, was an einem Beispiel belegt wird, das Elektroretinogramm nicht grundsätzlich erloschen zu sein. Es folgt die Darstellung elektroretinographischer Befunde bei einigen angeborenen Anomalien (Grubenpapille, Drusenpapille, markhaltige Nervenfasern), bei erblichen Sehnervenatrophien sowie bei Verletzungen des Sehnerven unter besonderer Berücksichtigung der erhaltenen oder unterbrochenen Netzhautzirkulation. Abschliessend Darlegung des objektiven Nachweises einer Dunkeladaptation an Augen, die durch Sehnervenleiden erblindet sind.

Abstract—This is a review of the literature on clinical electroretinographic findings in certain diseases of the optic nerve. As illustrated by an example, the electroretinogram need not necessarily be extinguished in cases of retinal atrophy. Electroretinographic findings are presented for a number of congenital anomalies (cupped disk, drusen papilla, myelinated nerve fibres), in extensive atrophies of the optic nerve, and in optic nerve injuries with special reference to the maintenance or disruption of retinal circulation. The paper concludes with an exposition of an objective proof of dark adaptation in eyes which were blinded by affections of the optic nerves.

Résumé—On rassemble, en dépouillant la littérature relative aux observations cliniques en électrorétinographie, divers résultats relatifs à des maladies du nerf optique. On fournit aussi un exemple où, dans un cas d'atrophie rétinienne, l'électrorétinogramme est insuffisant pour une interprétation exhaustive. Les observations électrorétinographiques sont ensuite données pour quelques anomalies innées (fond de la papille, glandes papillaires, fibres nerveuses médullaires) dans des atrophies héréditaires du nerf optique ainsi que dans des lésions du nerf optique sans autre considération que le maintien ou l'interruption de la circulation rétinienne. Pour terminer, on présente une épreuve objective de l'adaptation à l'obscurité d'un oeil qu'une affection du nerf optique achemine vers la cécité.

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DIE KLINISCHE Elektroretinographie (ERG), deren Entwicklung in erster Linie dem Stockholmer Ophthalmologen KARPE (1945) zu danken ist, gewährt bei einer Reihe von Krankheiten des Augenhintergrundes Einblicke in retinale Funktionsabläufe. GRANIT (1957), der die ERG von physiologischer Seite her durch entscheidende Erkenntnisse bereicherte, nennt unter denjenigen Situationen, bei denen das Elektroretinogramm (ERG) klinisch von Nutzen ist, vor allem "die Abwägung zwischen Netzhautkrankheit und Sehbahn- oder Gehirnstörung"; die Untersuchungen auf diesem Gebiet sind gleichzeitig ein Beitrag zu der Frage, an welchem Ort das ERG gebildet wird.

Klinisch ist es bisweilen bei einer Atrophie der Papille schwer und u.U. nicht zu entscheiden, ob man es mit einer aufsteigenden oder einer descendierenden Sehnervenatrophie zu tun hat. Das ERG gestattet im allgemeinen, diese wichtige und beispielsweise bei Gutachten u.U. entscheidende Frage zu beantworten, denn bisherige Ergebnisse lehren,

dass bei absteigenden Atrophien das ERG nach Einzelbelichtung normal zu sein pflegt, dagegen bei ascendierenden pathologisch ausfällt (KARPE, 1945; WADENSTEN, 1956; SCHMÖGER und THIEME, 1955; HENKES, 1957; FRANÇOIS, 1952; FRANCESCHETTI und DIETERLE, 1957).

Auch VANYSEK (1955) hat bei primären Sehnervenerkrankungen in erster Linie normale Netzhautpotentiale gefunden, bei zwei Patienten mit Neuritis N. optici waren allerdings die ERG subnormal. Pathologische Befunde dieser Art sind dann zu erwarten, wenn die Erkrankung des Sehnerven gleichzeitig die Retina in Mitleidenschaft zieht.

Dass aber das ERG möglicherweise auch durch zentral von der Netzhaut gelegene Stellen her beeinflusst werden kann, erscheint auf Grund des morphologisch und funktionell gelungenen Nachweises zentrifugaler Sehnervenfasern nicht ausgeschlossen. Dafür sprechen bestimmte experimentelle Untersuchungen:

So konnten beispielsweise JACOBSON und GESTRING (1958) zeigen, dass bei Katzen und Affen die *b*-Wellenamplitude nach Durchtrennung des N. opticus zunahm, ebenso nach der Verabreichung von Barbitursäurepräparaten. Dagegen wurde die *b*-Welle nach Hexamethonium-Gaben flacher. Eine Durchschneidung des Sehnerven brachte diesen Drogeneffekt zum Erlöschen. Dies weist auf die Existenz efferenter Impulse aus höheren Zentren hin.

Die Meinung, dass das ERG bei retinalen Atrophien stets erloschen, bei absteigenden dagegen erhalten sei, kann aber u.E. in dieser Form nicht beibehalten werden. Denn bei ascendierenden Atrophien braucht das ERG nicht immer ausgelöscht zu sein, es kann vielmehr auch subnormal ausfallen. Dazu ein Beispiel:

Arthur S., geboren 1892. Rechts frischer Zentralarterienverschluss, Visus Amaurose. ERG rechts subnormal, links normal. 15 Monate später rechts retinale Opticusatrophie, links Glaucoma chronic. simplex. Visus rechts Amaurose, links 5/7. ERG[1] rechts subnormal, links normal.

Zunächst zu unseren Befunden bei einigen angeborenen Anomalien: Bei der sog. *Grubenpapille* und der *Drusenpapille* ist das ERG normal. Einen interessanten Beitrag zur Sinnesphysiologie der Retina ergeben unsere Resultate bei *markhaltigen Nervenfasern* der Netzhaut. Bisher haben lediglich BJÖRK und KARPE (1951) über das ERG eines Patienten mit markhaltiger Nervenfaserbildung, allerdings bei gleichzeitiger Pseudoretinitis pigmentosa, berichtet. Der bei markhaltigen Nervenfasern vorhandene Gesichtsfeldausfall richtet sich erfahrungsgemäss nach dem von Markfasern bedeckten Netzhautgebiet. Es wäre deshalb eigentlich zu erwarten, dass bei einseitiger massiver markhaltiger Nervenfaserbildung eine Seitendifferenz mit einer am kranken Auge deutlich erniedrigten *b*-Wellenamplitude entsteht. Wie wir aber in den vier untersuchten einseitigen Fällen beobachten konnten, ist dies nicht der Fall.

Daraus geht hervor, wie sehr das nach unserer Methode abgeleitete klinische ERG einer komplexen Antwort der gesamten Retina entspricht. Das Fehlen einer erniedrigten *b*-Wellenamplitude bestätigt ausserdem von der elektrophysiologischen Seite her Befunde der pathologischen Anatomie. Denn der feingewebliche Bau der Netzhaut unter den markhaltigen Fasern ist normal. Das ERG zeigt, dass auch an denjenigen Stellen, an denen markhaltige Nerven vorhanden sind, Licht auf die darunter liegende, anatomisch intakte Netzhaut fallen muss.

Zur Frage des ERG bei *erblicher Sehnervenatrophie* liegen bisher nur wenige Berichte vor. DOLLFUS und CHALVIGNAC (1952) fanden bei einer Leberschen Atrophie supernormale Potentiale. FRANCESCHETTI und DIETERLE (1957) war es möglich, bei einer komplizierten Sehnervenatrophie des Kindesalters vom Typus Behr in zwei Fällen die ERG zu registrieren.

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[1] Die Potentiale wurden nach der früher von uns beschriebenen Methode abgeleitet (vgl. *Bibl. Ophthalm.* **48**, 137–160 (1957)).

Sie ermittelten eine relativ hohe *b*-Wellenamplitude. Wenngleich es auch bisher schon wohl als sicher feststand, dass es sich bei den hereditären Sehnervenatrophien um descendierende Opticusatrophien handelt, und daher beim Fehlen anderer Komplikationen kein abgeflachtes ERG erwartet werden durfte, stand bisher der entsprechende elektroretinographische Beleg an einem grösseren Material noch aus.

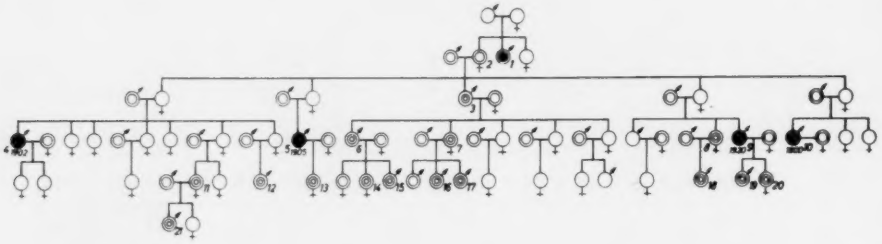

ABB. 1. Erbliche Sehnervenatrophie. Stammbaum einer Familie. Vier erkrankte und fünfzehn gesunde Angehörige konnten untersucht werden. Es sind folgende Symbole verwendet:

- ○ nicht untersucht,
- ◎ nicht untersucht, wahrscheinlich gesund;
- ◉ nicht untersucht, wahrscheinlich krank;
- ◎ untersucht, gesund;
- ● untersucht, krank.

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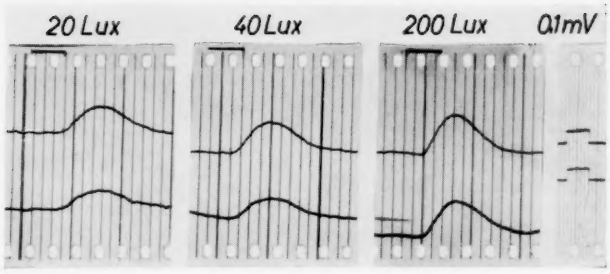
Wir konnten elf Patienten aus vier Familien mit erblicher Opticusatrophie untersuchen. In der ersten Familie sind vier erwachsene Männer erkrankt (Abb. 1). Die ERG fallen in drei Fällen beiderseits normal aus. Der Befund eines weiteren Mitglieds dieser Familie sei wegen der Besonderheit des Falles etwas eingehender beschrieben:

Peter W., geboren 1920. Im zweiten Weltkrieg Granatsplitterverletzung der linken Gesichtshälfte. Der Patient gilt daher als kriegsblind. Rechts träge und unausgiebige Lichtreaktion, einfache Sehnervenatrophie. Links amaurotische Pupillenstarre. Proliferierende Glaskörperschwarten vor der Papille und nasal davon. Visus rechts Handbewegungen vor dem Auge, links Amaurose. ERG (Abb. 2) beiderseits normal, aber links niedriger als rechts.

Die abgeflachten ERG des linken Auges sind hier als Symptom traumatischer Netzhautveränderungen, nicht aber der Sehnervenerkrankung, aufzufassen. Bei diesem Patienten haben wir die Potentiale auch im Verlauf der Dunkeladaptation abgeleitet. Trotz der Erblindung wird auch links während der Dunkeladaptation die *b*-Welle höher. Abb. 3 gibt diese Amplitudenzunahme bei der Reizintensität von 40 Lux wieder. Wie der Krankheitsverlauf am rechten Auge vermuten lässt, wäre links eine Herabsetzung des Sehvermögens infolge der familiären Sehnervenatrophie wohl sicher auch ohne die Verletzung zustande gekommen. Die Sehherabsetzung rechts und auch weitgehend links sind unserer Meinung nach nicht zurecht als Wehrdienstbeschädigung anerkannt. Die Lebersche Atrophie manifestierte sich zufällig während des Krieges. Dabei sei allerdings die Möglichkeit zugegeben, dass die Verletzung noch eine zusätzliche Schädigung des Sehnerven verursacht hat. Beispielsweise SCHMELZER (1957) berichtete über fünf Patienten in einer Sippe mit Leberscher Atrophie, von denen vier die Erkrankung auf einen Unfall bzw. eine Kriegsbeschädigung zurückführten, was von SCHMELZER (1957) angezweifelt wird. Gelegentlich könne allerdings eine besondere körperliche Anstrengung als Auslösungsmoment dienen.



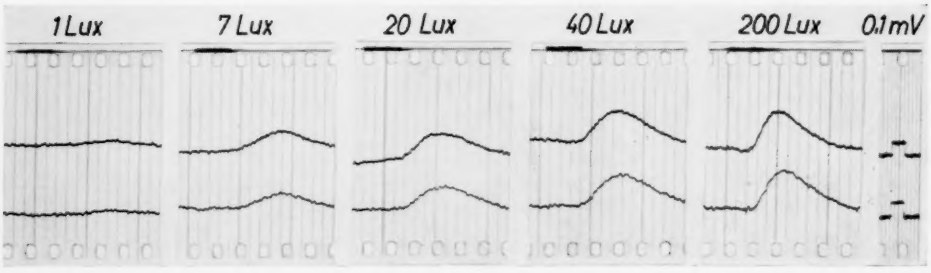


ABB. 2. Zum Vergleich normales ERG beider Augen bei den 5 verschiedenen Reizintensitäten. Obere Kurve ERG des rechten, untere Kurve ERG des linken Auges. Der schwarze Strich oben entspricht der Reizmarke. Ganz rechts Eichung. Die Höhe der Vertikalabweichung bedeutet 0,1 mV.
Darunter ERG eines Pat. mit Leberscher Opticusatrophie bei drei Reizintensitäten nach 12 Min Dunkeladaptation. Links ausserdem traumatische Glaskörper- und Fundusveränderungen. ERG beiderseits normal, aber links niedriger als rechts.

[*facing p.* 222]

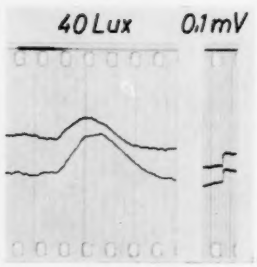


ABB. 4. Frische Abscherung des N. opticus mit Durchtrennung der Zentralarterie bei erhaltener cilio-retinaler Arterie rechts. ERG be 40 Lux beiderseits normal, rechts niedriger als links.

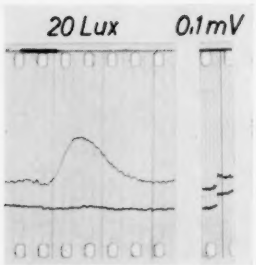


ABB. 5. Resektion des Sehnerven dicht hinter dem Bulbus wegen Opticusscheidenmeningiom links. Unterbrechung der Zentralarterie. ERG bei 20 Lux rechts normal, links ausgelöscht.

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In einer zweiten Familie ist das Leiden nicht geschlechtsgebunden bei vier Patienten in drei aufeinanderfolgenden Generationen teilweise schon in der Kindheit bzw. in der Jugend aufgetreten. Auch hier finden sich normale ERG. In einer dritten Familie sind Mutter und Sohn erkrankt. Die *b*-Wellen sind in dem einen Fall supernormal, in dem anderen normal. Schliesslich konnten wir eine jetzt 42-jährige Frau aus einer weiteren Familie erfassen, in der die erbliche Opticusatrophie ausschliesslich bei Frauen vorzukommen scheint. FRIEMANN (1949) hat bereits früher über diesen Stammbaum berichtet. Die Potentiale sind normal.

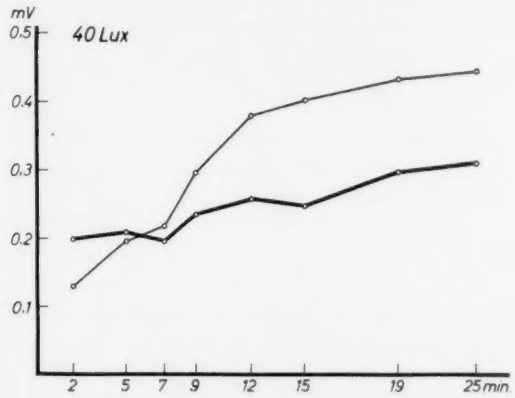

ABB. 3. Erbliche Sehnervenatrophie. Graphisch dargestellte Zunahme der *b*-Wellenhöhe eines erblindeten Auges im Verlauf der Dunkeladaptation bei der Reizstärke von 40 Lux. (Dünne Linie = normaler Vergleichswert eines gesunden Auges.)

Bei den an hereditärer Opticusatrophie Erkrankten ist also das ERG mit einer Ausnahme ebenso wie bei einer Reihe gesunder Familienangehöriger normal ausgefallen und zwar unabhängig vom Alter, Visus, Geschlecht, Manifestationstermin und Erbgang der Erkrankung, sofern keine begleitende Netzhautveränderung bestand. Damit ist der in dieser Form bisher noch fehlende Beweis erbracht, dass es sich bei den erblichen Opticusatrophien um absteigende Atrophien handelt. Dass darüberhinaus differentialdiagnostisch das ERG einen interessanten Beitrag zu dieser Krankheit leisten kann, zeigt die Tatsache, dass vor der Einführung der klinischen ERG eine enge Verwandtschaft zwischen der Amaurose des Kindes durch tapeto-retinale Degeneration und der infantilen Opticusatrophie vermutet wurde. Es handelt sich jedoch um Erkrankungen grundsätzlich verschiedener Art, denn bei jener, die eine aufsteigende Atrophie im Gefolge hat, ist das ERG von Anfang an erloschen.

Auch über das ERG bei *Verletzungen des Sehnerven* sind bisher nur wenige Untersuchungen bekannt. HENKES (1957) beobachtete bei einer Stauungspapille zunächst ein normales ERG. In den folgenden Monaten wurde die *b*-Welle höher. Nach der Entfernung eines Sehnerventumors erlosch das ERG. SUZUKI (1959) fand bei einem Patienten mit totaler Farbenblindheit und Durchtrennung des einen Sehnerven auf der verletzten Seite höhere Potentiale.

Wir haben unsere Beobachtungen unter dem Gesichtswinkel einer Unterbrechung bzw. des Erhaltenbleibens der Netzhautzirkulation klassifiziert. Zunächst ein Befund, bei dem die Netzhautdurchblutung nicht unterbrochen wurde:

Udo G., geboren 1933. Pfählungsverletzung der rechten Orbita mit schlagartiger Erblindung. Unmittelbar nach der Verletzung normaler Augenhintergrund, nahezu zwei Jahre später rechts Oculomotoriusparese, einfache Atrophie mit blasser Papille und engen Gefässen. Visus Amaurose. ERG beiderseits normal.

Diese Erblindung entstand durch eine Abscherung des Sehnerven zentralwärts von dem Eintritt der A. centralis retinae in den N. opticus. Die A. centralis retinae war seinerzeit, wie der ophthalmoskopische Befund auswies, normal. Allmählich entwickelte sich später eine absteigende (einfache) Atrophie mit sekundärer Engstellung der Gefässe, erwartungsgemäss fiel die *b*-Welle normal aus.

Bei einem anderen Patienten hat es sich um eine partielle Unterbrechung der arteriellen Netzhautzirkulation gehandelt:

Gerhard W., geboren 1945. Sturz mit dem Gesicht auf Fahrradlenkstange. Drei Tage danach rechts Protrusio bulbi mit Orbitalhämatom. Pupille übermittelweit, starr. Zentralarterienstammverschluss mit anämischen Arterienästen, ischämisches Ödem. Kleine blutführende cilio-retinale Arterie am temporalen Papillenrand. Visus rechts Amaurose. ERG (Abb. 4) beiderseits normal, aber rechts niedriger als links.

Hier hat man es mit einer Durchtrennung des Sehnerven mit Unterbrechung der Zentralarterie bei gleichzeitig vorhandener blutführender A. cilio-retinalis zu tun. Die *b*-Wellenhöhe am verletzten Auge ist zwar noch an der unteren Grenze des Normalen, fällt aber im Vergleich zur anderen Seite deutlich niedriger aus. Diese Abflachung des *b*-Potentials ist als Folge des Zentralarterienstammverschlusses aufzufassen. Beim nicht traumatischen Verschluss der A. centralis retinae sind die Potentiale oft, aber nicht immer, erloschen. In dem erwähnten Fall hat sicherlich noch die erhalten gebliebone A. cilio-retinalis dazu beigetragen, dass das ERG normal auspiel.

Schliesslich noch ein Beispiel einer Sehnervenverletzung, wobei die Zentralarterie unterbrochen und damit die Netzhautdurchblutung aufgehoben wurde:

Ursula B., geboren 1932. Links Exophthalmus, 5 dptr prominente Stauungspapille. Visus links Lichtschein, Projektion defekt. 3½ Monate später wurde links ein Opticusscheidenmeningiom entfernt: Resektion des Tumors auch orbitawärts mitsamt dem Sehnerven bis knapp hinter dem Bulbus. Jetzt links Bild des Stammverschlusses der Zentralarterie, ERG (Abb. 5) rechts normal, links ausgelöscht.

Bei den Verletzungen des N. opticus hängt das ERG von der Frage ab, ob die A. centralis retinae mit durchtrennt wurde. Das ERG gestattet daher, das Sehnerventrauma in Übereinstimmung mit dem ophthalmoskopischen Befund zu lokalisieren. Bekanntlich tritt die Zentralarterie erst kurz hinter dem Bulbus in den N. opticus ein. Bei erhaltener Netzhautdurchblutung mit zunächst normalem Fundus, später einfacher Atrophie lässt sich ein normales ERG ableiten. War die Zentralarterie unterbrochen, fanden wir erloschene Potentiale. Der Augenspiegelbefund zeigte dann einen Zentralarterienstammverschluss. Beim Vorhandensein einer intakten cilio-retinalen Arterie sind in einem solchen Fall die Potentiale niedriger als auf der gesunden Seite ausgefallen. Das ERG ist aber dann von besonderem Wert, wenn etwa nach einer Sehnervenverletzung wegen gleichzeitiger Trübungen der brechenden Medien der Fundus nicht eingesehen werden kann, denn Medientrübungen beeinträchtigen im allgemeinen die Netzhautpotentiale nicht oder nur unwesentlich.

Auf eine letzte Befundgruppe sei abschliessend noch hingewiesen. Durch das ERG lässt sich auch die Dunkeladaptation objektiv nachweisen, mit zunehmender Dunkeladaptation nimmt die Amplitude der *b*-Welle zu. Diese Empfindlichkeitszunahme braucht allerdings mit der subjektiven Schwellenempfindlichkeit nicht unbedingt parallel zu gehen. Über eine solche Beeinflussung des normalen ERG sind wir durch mehrere Arbeiten beispielsweise von KARPE und TANSLEY (1948); ALPERN und FARIS (1954); JOHNSON (1951); BEST und BOHNEN (1957); BORNSCHEIN (1953) unterrichtet.

Über den Verlauf des ERG während der Dunkeladaptation bei Erkrankungen des Auges liegen aus neuerer Zeit einige Berichte vor: VANYSEK (1955) bei Glaukom und sklerotischer

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Maculadegeneration, HENKES, VAN DER KAM und WESTHOFF (1954) bei sklerotischen Fundusveränderungen, ELENIUS und HECK (1958) bei Achromatopsie, GOODMAN und GUNKEL (1958) sowie SKEEHAN, PASSMORE und ARMINGTON (1957) bei Retinitis pigmentosa, BURIAN (1953, 1954, 1957, 1958) bei Pseudoretinitis pigmentosa, BOUNDS und JOHNSTON (1955) bei Chorioideremie, RENDAHL (1958) bei angeborener Hemeralopie, Protanopie und totaler Farbenblindheit, FRANÇOIS und VERRIEST (1952, 1958), ARMINGTON und SCHWAB (1954) sowie RIGGS (1954) bei Hemeralopie, JAYLE (1958) bei sog. seniler Maculadegeneration. Untersuchungen an blinden Augen wurden dagegen u.W. bislang von anderer Seite noch nicht vorgenommen.

Deshalb interessierte uns die Frage, ob überhaupt und gegebenenfalls in welcher Weise sich auch an *erblindeten Augen* ein *Adaptationsvorgang* nachweisen lässt. Selbstverständlich scheidet hier die subjektive Untersuchung am Adaptometer auch als Kontrollmöglichkeit aus.

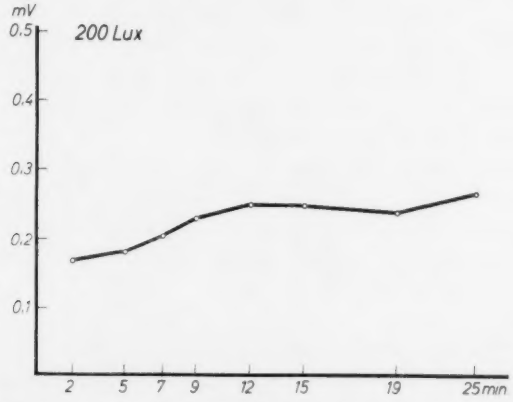

ABB. 6. Seit 10 Jahren absolutes Glaukom. ERG erhalten. Zunahme der *b*-Wellenamplitude während der Dunkeladaptation.

Wir haben blinde Augen von vorerst siebzehn weiteren Patienten untersucht, bei denen die Amaurose auf ein Sehnervenleiden (in diesem Zusammenhang sei darunter auch das absolute Glaukom verstanden) zurückzuführen ist: sechs absolute Glaukome und elf absteigende Opticusatrophien (sieben traumatische, zwei nach Neuritis und je einer bei Hypophysentumor und Arteriitis temporalis). Die Klassifizierung der ERG dieser Augen, wie sie sich bei der üblichen Routineuntersuchung ergab, umfasst alle Typen des klinischen ERG von ausgelöscht bis supernormal.

Zunächst zu den absoluten Glaukomen: Bei drei Augen mit teilweise sichtbaren komplizierenden intraokularen Veränderungen sind die ERG erloschen und bleiben es auch mit zunehmender Dunkeladaptation. Aber in drei anderen Fällen finden wir subnormale oder normale *b*-Wellen. Dabei entsteht im Verlauf der Dunkeladaptation eine deutliche Amplitudenzunahme der *b*-Potentiale (Abb. 6). Diese Amplitudenzunahme ist der Ausdruck einer indes nur noch teilweise intakten Retina, denn sie erfolgt nicht in normaler Weise. Man darf daraus folgern, dass beim absoluten Glaukom eine individuell verschieden stark ausgeprägte Schädigung der Retina selbst, und zwar auch ihrer peripheren Partien, vorhanden ist.

Anders dagegen verhält es sich bei der absteigenden Opticusatrophie mit Amaurose, wie dies bei sieben Patienten nach Verletzungen der Fall ist. Das Datum der Verletzung liegt

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dabei bis zu 40 Jahren zurück. Die ERG sind in fünf Fällen normal und nehmen im Verlauf der Dunkeladaptation deutlich zu.

Wenn aber, wie wir das in einem Fall beobachteten, bei der Verletzung gleichzeitig mit der Unterbrechung des Sehnerven noch traumatische Netzhaut- und Aderhautveränderungen gröberer Art entstanden sind, so fallen die ERG subnormal aus. Bei einer traumatischen Atrophie ermittelten wir trotz der Amaurose bei einigen Reizintensitäten sogar supernormale *b*-Potentiale. Auch in diesen beiden Fällen kommt es zu einer Vergrösserung der *b*-Wellenamplitude im Verlauf der Dunkeladaptation.

Eine Zunahme der *b*-Wellenhöhe während der Dunkeladaptation fanden wir noch in den drei Fällen, in denen es sich um eine Erblindung im Verlauf einer Neuritis N. optici, durch eine Opticusatrophie bei Hypophysentumor und eine Sehnervenatrophie bei Arteriitis temporalis gehandelt hat.

Fassen wir diese Befunde zusammen, so zeigt sich, dass sich bei blinden Augen mit Hilfe des ERG, und zwar ausschliesslich durch diese Methode, Vorgänge der Dunkeladaptation in der Netzhaut objektivieren lassen, sofern noch funktionstüchtige Sehelemente vorhanden sind. Man kann so, selbst wenn etwa wegen Trübungen der brechenden Medien der Augenhintergrund nicht mehr eingesehen werden kann, feststellen, ob gleichzeitig auch eine Schädigung der Netzhaut besteht. Die Differenzierung, ob die Ursache einer Erblindung in der Netzhaut oder zentralwärts davon gelegen ist, scheint durch das ERG leichter, wenn man es im Verlauf der Dunkeladaptation untersucht.

Diese wenigen Beispiele aus dem Kapitel der Veränderungen des Sehnerven mögen genügen zu zeigen, dass der ERG neben ihrem theoretischen Wert auch eine wichtige praktische Bedeutung zukommt.

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DAS ADAPTIVE VERHALTEN DER FROSCHNETZHAUT, UNTERSUCHT MIT DER METHODE DER KONSTANTEN ELEKTRISCHEN ANTWORT[1]

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Zusammenfassung—Mit der Methods der konstanten Antwort im Elektroretinogramm wurde das adaptive Verhalten der Froschnetzhaut untersucht. Geprüft wurde die Änderung der Reizschwelle *a*—während Dunkeladaptation nach verschieden starker Helladaptation und für Testreize verschiedener Wellenlänge *b*—während Helladaptation bei Konstanter adaptiver Beleuchtung und in Abhängigkeit von der adaptiven Beleuchtungsstärke.

Abstract—Dark- and light-adaptation has been measured in frogs by determining the light energy necessary to produce a constant small *b*-wave in the electroretinogram.

Dark-adaptation after 30 min exposure to lights up to 10^3 times dark threshold proceeds as a single fast process. After light-adaptation to a somewhat higher intensity dark-adaptation is completed in about the same period of time but there is, in addition, a break in the dark-adaptation curve separating two phases with a different rate of change of threshold. Bipartite dark-adaptation curves with a slow change of threshold after the break are seen only after exposure to light intensities for which appreciable bleaching of visual pigment is reported. The speed of dark-adaptation after the break is inversely proportional to the intensity of the adapting light.

After exposure to strong light, dark-adaptation for coloured lights shows bipartite curves for all wavelengths between 401 and 652 mμ. The break separating the two phases of dark-adaptation occurs earlier, and the total change of threshold is larger for blue light of 462 mμ than for stimuli of any other wavelength, including violet light. The threshold variations during dark-adaptation up to the break are almost parallel for lights of all wavelengths. With the beginning of the second phase of dark-adaptation in response to blue light there is a definite rise of threshold in response to red light. This depressing effect lasts until the relative thresholds for red and blue are the same as in the fully dark-adapted state.

The change of threshold of fully dark-adapted frog's eye during light-adaptation is measured in two different ways.

By the first procedure the time course of light-adaptation after exposure to strong light is recorded. Directly after the onset of light-adaptation a large increase of threshold is seen. This is followed by an opposite change of threshold of more than one log unit between 5 sec and 10–20 min in the light, half of which being completed within 30 sec. Most of this change can be ascribed to photomechanical movement of pigment-granula because frogs adrenalized in the dark-adapted state exhibited a higher absolute threshold and showed only a fraction of this fall of threshold during light-adaptation.

In the second procedure the retinal illumination (I) is increased in steps of 0·6 log units and the increment threshold (dI) is measured for test lights of different wavelengths. Within an adaptive range of 7·2 log units the ratio of log dI/log I is small (0·5) for 605 mμ and larger (0·75) for 462 mμ. After correction is made for the shielding effect of the photomechanical movement of the pigment-granula the increment threshold in response to 462 mμ is about of the same order as the increase of adaptive illumination.

Proceeding from dark- to light-adaptation the luminosity curve is measured at different levels of adaptive illumination. The earliest sign of a Purkinjé shift appears at a retinal illumination of about 10 times dark threshold. At a 10^3 times higher illumination

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a mesopic sensitivity curve is obtained with a maximum in the green and with humps in the blue and the orange. At 10^5 times dark threshold the highest sensitivity is recorded between 584 and 605 mμ. Further increase of retinal illumination decreases the breadth of the sensitivity curve without affecting the spectral position of the maximum.

Résumé—L'adaptation à l'obscurité et à la lumière a été mesurée sur des grenouilles en déterminant l'énergie lumineuse nécessaire pour produire une petite onde *b* constante dans l'électrorétinogramme.

Après 30 minutes d'exposition à des lumières inférieures à mille fois le seuil absolu, l'adaptation à l'obscurité progresse comme un processus simple. Après adaptation à la lumière à des niveaux plus élevés, l'adaptation à l'obscurité est terminée à peu près dans le même temps, mais on constate en outre un point anguleux dans la courbe d'adaptation à l'obscurité, séparant deux phases dont la vitesse de variation du seuil est différente. Les courbes d'adaptation à l'obscurité bipartites avec un lent changement du seuil après le point anguleux ne s'observent qu'après exposition à des intensités lumineuses qui produisent une décoloration appréciable du pigment visuel. La vitesse de l'adaptation à l'obscurité après le point anguleux est inversement proportionnelle à l'intensité de l'adaptation lumineuse.

Après exposition à une lumière intense, l'adaptation à l'obscurité pour des lumières colorées produit des courbes bipartites pour toutes les longueurs d'onde entre 401 et 652 mμ. La séparation entre les deux phases de l'adaptation à l'obscurité se produit plus tôt et la variation totale du seuil est plus grande pour la lumière bleue 462 mμ que pour des stimuli d'une autre longueur d'onde, y compris la lumière violette. Les variations du seuil pendant l'adaptation à l'obscurité sont presque parallèles pour toutes les longueurs d'onde jusqu'au point anguleux. Au début de la seconde phase d'adaptation à l'obscurité en lumière bleue, il se manifeste une nette élévation du seuil en réponse à une lumière rouge. Cet effet inhibiteur continue jusqu'à ce que les seuils pour le rouge et le bleu soient les mêmes en valeur relative comme dans l'état de complète adaptation à l'obscurité.

Pour l'oeil de grenouille complètement adapté à l'obscurité, la variation du seuil pendant l'adaptation à la lumière est mesurée de deux façons différentes.

Dans la première méthode on enregistre le changement avec le temps de l'adaptation à la lumière après exposition à une lumière intense. Juste après le début de l'adaptation à la lumière, on observe une forte augmentation du seuil. Puis on constate un changement en sens inverse du seuil, de plus d'une unité log, entre 5 sec et 10–20 min de lumière, la moitié étant terminée en 30 sec. La plus grande partie de ce changement est attribuable au mouvement photomécanique des granules pigmentaires, parce que l'action de l'adrénaline sur la grenouille dans l'état d'adaptation à l'obscurité produit une élévation du seuil absolu et une fraction seulement de la chûte du seuil pendant l'adaptation à la lumière.

Dans la seconde méthode l'éclairement rétinien (I) est augmenté par échelons de 0,6 unités log et on mesure le seuil différentiel (dI) pour des tests de différentes longueurs d'onde. Dans un intervalle d'adaptations de 7,2 unités log, le rapport dI/I est petit (0,5) pour 605 mμ et plus grand (0,75) pour 462 mμ. Après correction de l'effet d'écran dû au mouvement photomécanique des granules pigmentaires, le seuil différentiel pour 462 mμ devient du même ordre de grandeur que l'accroissement de l'éclairement d'adaptation, c'est-à-dire que la loi de Weber est vérifiée (dI/I = const.).

En passant de l'adaptation à l'obscurité à celle à la lumière la courbe d'efficacité lumineuse est mesurée à différents niveaux de l'éclairement d'adaptation. Le premier signe d'un effet Purkinjé apparait pour un éclairement rétinien de 10 fois le seuil absolu environ. Pour un éclairement 10^3 fois plus élevé on obtient une courbe de sensibilité mésopique avec maximum dans le vert et des bosses dans le bleu et dans l'orange. A 10^5 fois le seuil absolu la plus haute sensibilité est obtenue entre 584 et 605 mμ. Si l'on augmente encore l'éclairement rétinien, la largeur de la courbe de sensibilité diminue sans que la position spectrale du maximum soit changée.

DAS FROSCHAUGE ist seit jeher Gegenstand intensiver physiologischer Untersuchungen gewesen, nicht zuletzt wegen seiner in mehrfacher Hinsicht verblüffenden Ähnlichkeit zur menschlichen Netzhaut. Eine Untersuchung der beim Frosch während Dunkel- und Helladaptation stattfindenden Änderungen der Reizschwelle ist daher ausser von vergleichend-physiologischem Interesse auch von praktischer Bedeutung, da die beim Frosch

anzuwendende elektroretinographische Adaptationsmessung auch am menschlichen Auge verwandt werden kann.

In der Mehrzahl der bisherigen elektroretinographischen Untersuchungen über das adaptive Verhalten der Netzhaut wurde die *b*-Welle als Antwort auf Lichtreize konstanter Intensität während Dunkel- und Helladaptation registriert (ELENIUS, 1958). Ein Vergleich zwischen elektroretinographischen und sensorischen Dunkeladaptationskurven ist jedoch nur auf der Basis der Reizschwelle möglich, d.h. durch Messung der für konstante, schwellennahe Antworten notwendigen Energie. Eine Umrechnung der mit der Methode des konstanten Reizes gewonnenen Resultate in Reizschwellenkurven macht Schwierigkeit, da die Beziehung zwischen Potentialhöhe und Stärke des Testreizes mit dem Adaptationszustand variiert und beide Grössen nur innerhalb eines relativ engen Intensitätsbereiches proportional sind (DODT und ECHTE, 1961). Für den Frosch geben lediglich die Messungen von RIGGS (1937) den Verlauf der Reizschwellenänderung im Elektroretinogramm während Dunkeladaptation wieder. Riggs beobachtete nach intensiver Helladaptation während des nachfolgenden Dunkelaufenthaltes eine ähnliche Zweiteilung der Adaptationskurve wie sie von AUBERT (1865) erstmals beim Menschen beschrieben wurde und nach KOHLRAUSCH (1922) den Übergang der Zapfen- zur Stäbchenadaptation anzeigt.

Nachfolgend wird die von RIGGS (1937) und ELENIUS und DODT (1960) benutzte Methode der konstanten elektroretinographischen Antwort verwandt, um die Veränderung der Reizschwelle des Froschauges während Dunkeladaptation nach verschieden starker Helladaptation und für Testreize verschiedener Wellenlänge zu untersuchen. Anschliessend wird mit der gleichen Methode das Verhalten der Reizschwelle während Helladaptation untersucht. Dabei wird sowohl die zeitliche Änderung der Reizschwelle für eine konstante adaptive Beleuchtung bestimmt, als auch die Änderung der Reizschwelle in Abhängigkeit von der adaptiven Beleuchtungsstärke.

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METHODE

Präparation

Ausgewachsene, über Nacht dunkeladaptierte Winter- und Sommerfrösche (R. tempor.) wurden untersucht. Nach Immobilisierung durch Tubocurarin (0,1 mg/g) wurde die Cornea entfernt, die Iris durch radiäre Einschnitte erweitert und das Tier in eine abgeschirmte Kammer verbracht, deren Temperatur vor und während des Versuchs durch einen Wasserdurchlauf auf 17°C einreguliert wurde. Die Haut des Tieres wurde mit feuchter Gaze bedeckt. Zur Aufrechterhaltung der Atmung wurde ein konstanter Strom von Sauerstoff zugeführt. Die Präparation wurde unter dunkelrotem Licht (Jena RG 5) durchgeführt. Anschliessend wurde erneut dunkeladaptiert, bis Konstanz der Reizschwelle im Elektroretinogramm festgestellt wurde.

Lichtreizung

Das zur Lichtquelle hin gerichtete Auge erhielt seine Reize von einer Mattscheibe von 1,5 cm Durchmesser in 1 cm Entfernung vom Auge. Die Mattscheibe wurde von einem mittels Xenonlampe (45A/1000 W) betriebenem Zweistrahl-Adaptometer ausgeleuchtet. Von den beiden Strahlen des Geräts diente der eine zur Lichtadaptation, der andere zur Bestimmung der Reizschwelle. Unterbrechung und Freigabe beider auf die Mattscheibe gerichteten Lichtstrahlen erfolgte über ein elektronisches Reizgerät und zwei elektromechanische Verschlüsse. Die Testreize (Dauer 40 msec) konnten entweder für sich (zur Messung der absoluten bzw. der Unterschiedsschwelle) oder in beliebigem, konstanten zeitlichen

Abstand nach Verdunklung des Adaptationsstrahles (zur Messung der Schwellenveränderung während der ersten Sekunden der Dunkeladaptation) ausgelöst werden. Das optische System des Adaptometers bestand aus Kondensoren, Linsen und Spiegeln. Zur Aussonderung der Wärmestrahlung wurden Wärmeabsorptionsgläser verwandt, zur Herstellung monochromatischen Lichtes im Bereich 401–693 mμ dienten Doppel-Interferenzfilter. Die Kontrolle der Lichtintensität erfolgte durch Neutralfilter, deren optische Dichte für die benutzten Wellenlängen spektrophotometrisch bestimmt wurde. Zur Eichung der relativen Strahlungsleistungen im Spektrum wurde ein Vacuum-Thermoelement mit einem empfindlichen Galvanometer als Anzeige verwandt.

Ableitung

Die Ableitung der Potentiale erfolgte zwischen Bulbus und Schädeldach vermittels in Kochsalzlösung angefeuchteter Baumwollfäden und Silber-Silberchlorid-Elektroden. Die Potentiale wurden einem Differential-Vorverstärker zugeführt und auf einem Kathodenstrahloszillographen photographisch registriert. Die Zeitkonstante des Verstärkers betrug 0,5 sec; zur Beobachtung der Potentialform wurde in einigen Versuchen Gleichstromverstärkung verwandt. Zur Markierung des Reizes wurde ein Teil des Lichtstrahls durch Spiegel auf eine Photozelle reflektiert, die über einen Vorverstärker mit dem zweiten Strahl des Oszillographen verbunden war.

Messungen

Zur Messung der Reizschwelle (absolute Schwelle und Unterschiedsschwelle) wurde durch Aufzeichnung der *b*-Welle gegen die Lichtreizintensität (optische Dichte der Neutralfilter) die für eine konstante Antwort von 20 μV notwendige Energie festgestellt. Dabei wurde die Amplitude der *b*-Welle entweder von der Nullinie (bei monophasischen Potentialen) oder von der Senke der *a*-Welle (bei mehrphasischen Potentialen) gemessen. Jene Lichtenergie, die nach 12-stündiger Dunkeladaptation ein Potential von 20 μV auslöste, wurde als Dunkelschwelle (Null Ordinate) bezeichnet. Die zeitlichen Veränderungen der Reizschwelle während Dunkel- und Helladaptation und die Unterschiedsschwellen wurden in Abhängigkeit von der Dunkelschwelle aufgezeichnet. Zur Bestimmung der spektralen Empfindlichkeitskurve wurde die bei Reizung mit verschiedenen Wellenlängen für eine Antwort von 20 μV notwendige Energie gemessen, wobei jeweils nach zwei Wellenlängen eine Kontrolle mit einer konstanten Wellenlänge vorgenommen wurde. Die für verschiedene Wellenlängen erhaltenen relativen Energien wurden für ein Spektrum gleicher Quantenzahl korrigiert und auf die Kontrolle bezogen als relative Sensitivitäten berechnet.

Photometrie

Die wirksame Öffnung der operativ erweiterten Pupille betrug 20 mm^2. Als Leuchtdichte das Adaptationsstrahles wurden bei voller Lichtstärke hinter der Mattscheibe 2620 candela/m^2 gemessen. Somit betrug die maximale retinale Beleuchtung $5{,}24 \cdot 10^4$ Trolands. Die Intensität des Teststrahles war etwa 10-mal grosser. Im dunkeladaptierten Zustand war die wirksame Strahlung für 507 mμ etwa 1/100 jener des ungefilterten, weissen Lichtes.

ERGEBNISSE

(1) *Die Darstellung des Adaptationsverlaufs*

Zur zahlenmässigen Charakterisierung des Adaptationsverlaufs wird bei sensorischer

Prüfung allgemein die für eine eben wahrnehmbare Helligkeitsempfindung notwendige physikalische Strahlungsintensität bestimmt. Dieses im Prinzip auch bei elektroretinographischer Schwellenbestimmung anwendbare Verfahren ist jedoch weniger genau als die Bestimmung der für ein Potential konstanter Höhe erforderlichen Lichtenergie. Da die Amplituden-Intensitätskurven der *b*-Welle bei verschiedener Farbe der Testreize und bei verschiedener retinaler Beleuchtung nicht strikt parallel sind (vgl. Abb. 5), wurde hierzu die kleinste, exakt messbare Antwort im Elektroretinogramm (20 μV) verwandt. Der Verlauf der Dunkel- und Helladaptation wurde als Änderung der relativen Energie der Testreize für diese konstante Antwort von 20 μV (im Folgenden als Reizschwelle bezeichnet) gegenüber der Dunkelschwelle (relative Energie für eine ebensolche Antwort im voll dunkeladaptierten Zustand = Null Ordinate) aufgezeichnet.

In der Regel wird der Verlauf der Dunkeladaptation in Form einer Kurve beschrieben, die den Logarithmus der Reizschwelle (oder ihre Kehrwertes) zur Dauer des Dunkelaufenthalts in Beziehung setzt (BEST, 1910). Dieser halblogarithmische Masstab ist zur Darstellung ausreichend, falls die erste Messung der Reizschwelle während Dunkeladaptation nicht früher als etwa 30 Sekunden nach Ende der Helladaptation erfolgt. Innerhalb dieses Zeitraums sind jedoch Änderungen der Reizschwelle von mehreren Dekaden keine Seltenheit (DODT und JESSEN, 1961), und zur genauen Darstellung derartig schneller Veränderungen der Reizschwelle ist eine logarithmische Zeitachse zweckmässig (KOHLRAUSCH, 1931).

Zur Darstellung der Besonderheiten der im Folgenden durchgehend benutzten doppellogarithmischen Aufzeichnung der Adaptationskurven ist in Abb. 1 ein und derselbe Versuch vergleichsweise in halblogarithmischer (A) und in doppellogarithmischer (B)

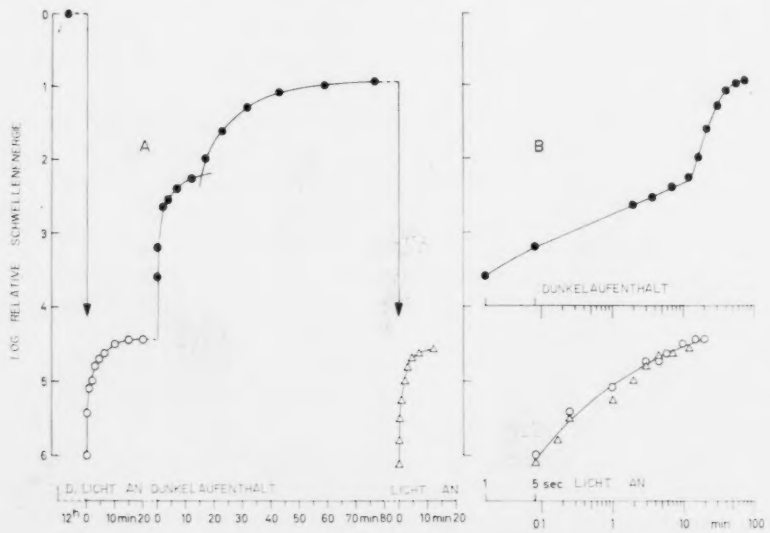

ABB. 1. Zeitlicher Verlauf von Hell- und Dunkeladaptation in halblogarithmischer (A) und doppellogarithmischer Darstellung (B). Ordinate: Relative Energie weissen Lichts für eine Antwort im Elektroretinogramm von 20 μV. Abszisse: Adaptationsdauer. Ein für 12 Stunden dunkeladaptiertes Froschauge (Reizschwelle = Null-Ordinate) wird nacheinander helladaptiert (offene Kreise), dunkeladaptiert (gefüllte Kreise) und erneut helladaptiert (offene Dreiecke). Retinale Beleuchtung während Helladaptation: $1{,}3 \cdot 10^4$ Trolands.

Darstellung wiedergegeben. Ein für 12 Stunden dunkeladaptiertes Froschauge wurde nacheinander helladaptiert, dunkeladaptiert, und schliesslich erneut helladaptiert. Die Messpunkte bezeichnen die Änderungen der Reizschwelle während Dunkeladaptation (gefüllte Kreise) und während Helladaptation (offene Symbole). Mit einsetzender Helladaptation ($1{,}3 \cdot 10^4$ Trolands) steigt die für eine konstante Antwort von 20 μV benötigte Energie unmittelbar sehr stark an und beträgt nach 5 Sek Helladaptation etwa das 10^6-fache der Dunkelschwelle. Zwischern der fünften Sekunde und der zwölften Minute der Helladaptation (offene Kreise) sinkt die Reizschwelle um etwa das 32-fache, wobei sich bei arithmetischer Zeitachse ein exponentieller, bei logarithmischer Zeitachse ein fast linearer Verlauf zeigt. Ein ähnlicher Verlauf ist auch während Dunkeladaptation zu beobachten, wobei sich die Energie des Testreizes zwischen der fünften Sekunde und der zwölften Minute auf 1/10 vermindert, dem jedoch bereits während der ersten 5 Sek Dunkeladaptation eine Senkung der Reizschwelle auf 1/17 des während Helladaptation gemessenen Wertes vorausgeht. Sowohl in der halblogarithmischen als auch in der doppellogarithmischen Darstellung ist nach 15 Min Dunkeladaptation ein Knick zu erkennen, dem eine zweite Adaptationsphase folgt. Dabei ist das Verhältnis der Steilheit der Reizschwellenänderung vor und nach dem Knick je nach Darstellungsart verschieden, doch ist der Zeitpunkt des Knicks in beiden Fällen konstant.

(2) *Verlauf der Dunkeladaptation nach verschiedener Helladaptation*

Nach Beobachtungen beim Menschen ist der Verlauf der Dunkeladaptation von der Dauer und Intensität der vorausgehenden Helladaptation abhängig (MÜLLER, 1931; HECHT, HAIG und CHASE, 1937; WALD und CLARK, 1937). Für den Frosch ist in Abb. 2 die Änderung der Reizschwelle nach Helladaptation konstanter Dauer (30 Min) und verschiedener Intensität wiedergegeben. Am Ende der Helladaptation an ein schwaches Licht (0,4 Trolands = offene Dreiecke) ist die Schwelle um das 40-fache gegenüber der Dunkelkontrolle gesteigert, kehrt jedoch innerhalb 15 Min bis auf das 3-fache der ursprünglichen Dunkelschwelle zurück. Dabei ergibt sich bei doppellogarithmischer Darstellung eine annähernd lineare Beziehung zwischen der Schwellenveränderung und der Dauer der Dunkeladaptation. Nach Helladaptation an ein 8-mal stärkeres Licht (3,3 Trolands, offene Kreise) und an ein 64-mal stärkeres Licht (26 Trolands, offene Quadrate) ist die Änderung der Reizschwelle bei Dunkeladaptation wesentlich grösser, während die totale Adaptationszeit praktisch gleich bleibt. Auch hier besteht angenähert eine lineare Beziehung zwischen der Schwellenveränderung und der Dauer der Dunkeladaptation.

Einen teilweise anderen Verlauf zeigt die Dunkeladaptationskurve nach stärkerer Helladaptation. Nach 210 Trolands (gefüllte Dreiecke) ist in der Dunkeladaptationskurve ein diskontinuierlicher Verlauf mit einem Knick bei etwa einer Minute zu sehen; nach Helladaptation mit 3300 Trolands (gefüllte Kreise) und 52 400 Trolands (gefüllte Quadrate) ist diese Zweiteilung der Dunkeladaptationskurve noch deutlicher; ausserdem erscheint hier die totale Adaptationszeit beträchtlich verlängert. Auffallend ist die mit stärkerer Helladaptation zunehmende Änderung der Reizschwelle während der ersten Sekunde der Dunkeladaptation. Während bei mässiger Helladaptation die während dieser und nach einer Sekunde Dunkeladaptation gemessenen Reizschwellen praktisch gleich sind (offene Symbole), sinkt die Reizschwelle nach stärkerer Helladaptation innerhalb der ersten Sekunde der Dunkeladaptation auf 1/2 bis 1/16 der während Helladaptation gemessenen Werte (gefüllte Symbole).

Der bei stärkerer Helladaptation nach dem Knick sichtbare Teil der Dunkeladaptationskurve ist offenbar der gleiche Prozess, der bei mässiger Helladaptation allein den Verlauf der Reizschwellenkurve bestimmt (Abb. 2, ausgezogene Linien). Für diese Annahme spricht einmal der lineare, mit zunehmender Helladaptation stärker verzögerte Verlauf dieses Prozesses. Zum anderen sind während Dunkeladaptation bis zum Knick schnelle diphasische, "photopische" Potentiale zu sehen, während nach dem Knick in der Dunkeladaptationskurve langsame, monophasische "skotopische" Potentiale registriert werden.

Der Knick in der Dunkeladaptationskurve ist nicht immer so deutlich wie in den bisher beschriebenen Versuchen. Er lässt sich jedoch in der doppellogarithmischen Darstellung relativ leicht lokalisieren, wozu ganz besonders die Messungen während der ersten Minute der Dunkeladaptation beitragen. Bei ein und derselben Netzhaut wird der Knick umso früher beobachtet, je stärker die Beleuchtung während Helladaptation ist. Dabei ergibt sich bei doppellogarithmischer Aufzeichnung eine lineare Beziehung zwischen der Reizschwelle am Ende der Helladaptation und dem Zeitpunkt des Knicks (Abb. 3).

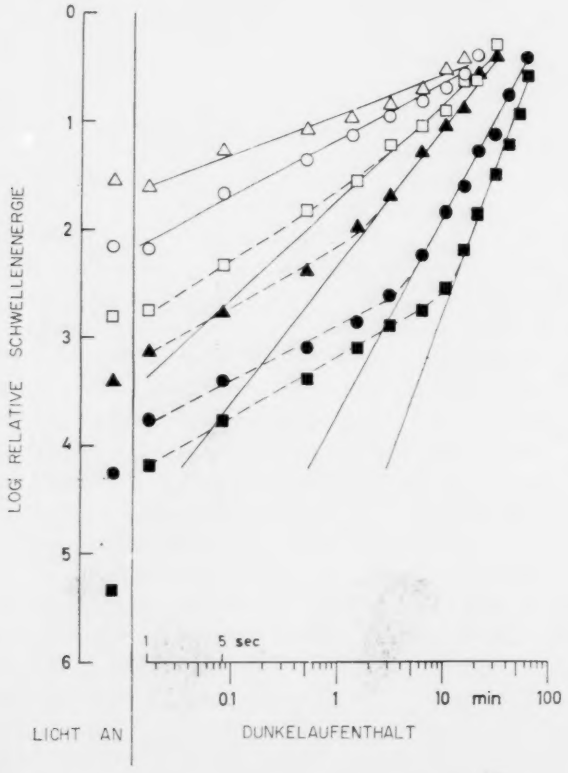

ABB. 2. Dunkeladaptationskurven eines Frosches nach verschieden starker Helladaptation konstanter Dauer (30 Min). Retinale Beleuchtung während Helladaptation: 0,4 Trolands = offene Dreiecke; 3,3 Trolands = offene Kreise; 26 Trolands = offene Quadrate; 210 Trolands = gefüllte Dreiecke; 3300 Trolands = gefüllte Kreise; 52400 Trolands = gefüllte Quadrate. Ordinate: Relative Energie weissen Lichts für eine Antwort im Elektroretinogramm von 20 μV, Null-Ordinate = relative Energie für eine Antwort von 20 μV nach 12 Stunden Dunkeladaptation.

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(3) *Verlauf der Dunkeladaptation für Testreize verschiedener Wellenlänge*

Zur elektroretinographischen Messung der Dunkeladaptationskurve des Frosches für verschiedenfarbige Testreize wurden die Reizschwellen für die einzelnen Wellenlängen zunächst während Dunkeladaptation, dann gegen Ende der nachfolgenden Helladaptation (30 Min Dauer, $1{,}3 \cdot 10^4$ Trolands) bestimmt. Während des anschliessenden Dunkelaufenthaltes wurde die Schwelle zunächst für weiss und zwei beliebige Wellenlängen verfolgt. Nach 90 Min Dunkeladaptation wurde das Auge wie zuvor helladaptiert, anschliessend die Messung bei Dunkeladaptation für weiss und zwei andere Wellenlängen wiederholt und in eben derselben Weise nochmals für weiss und zwei weitere Wellenlängen verfahren. Auf diese Weise wurden die Reizschwellen für 652, 605, 552, 507, 462, 418 und 401 mμ bestimmt. Zur gemeinsamen Darstellung wurden die gemessenen relativen Energien auf weiss als Kontrolle bezogen als Änderung gegenüber der Dunkelschwelle aufgezeichnet (Abb. 4).

In Übereinstimmung mit früheren Untersuchungen beim Menschen (KOHLRAUSCH, 1922) und beim Frosch (GRANIT, 1942; DONNER und RUSHTON, 1959) sind die während Helladaptation auftretenden Abweichungen der Reizschwelle gegenüber der Dunkelkontrolle für kurzwellige Lichtreize am grössten und bleiben während der Dunkeladaptation für langwellige Lichtreize am längsten nachweisbar. Erst nach 50 Min Dunkeladaptation erreicht die relative Reizschwelle für 652 mμ die gemeinsame Kontrolle, während dies für 605 mμ schon nach 30 Min und für 552 mμ nach 20 Min der Fall ist. Anschliessend findet keine Verschiebung der relativen Reizwerte zueinander mehr statt, man beobachtet lediglich eine allgemeine Senkung der Reizschwellen in Richtung auf die zu Beginn des Versuches gemessene Dunkelkontrolle (Null Ordinate).

Während der ersten Phase der Dunkeladaptation besteht die grösste Abweichung gegenüber der Dunkelschwelle für Blau (462 mμ). Dies bestätigt die Beobachtungen von

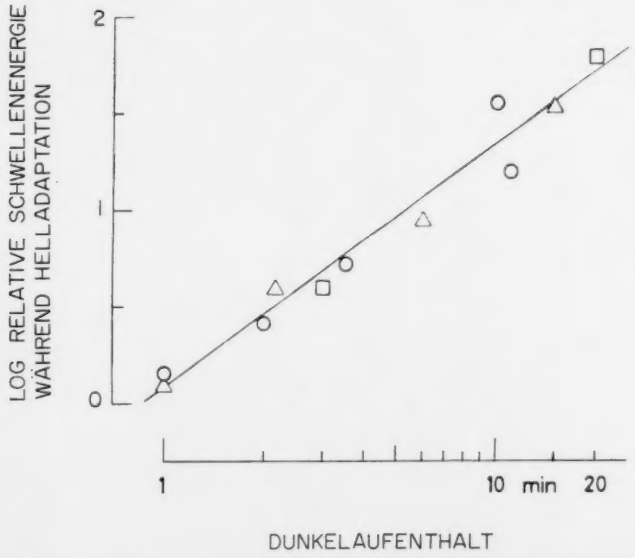

ABB. 3. Zeitpunkt des Knicks in der Dunkeladaptationskurve des Frosches (Abszisse) nach verschieden starker Helladaptation konstanter Dauer (30 Min). Ordinate: Relative Reizschwelle (Lichtenergie für eine Antwort im Elektroretinogramm von 20 μV) am Ende der Helladaptation. Verschiedene Versuche, durch Symbole gekennzeichnet.

KOHLRAUSCH (1922), wonach die spektrale Augenempfindlichkeit während der ersten Phase der Dunkeladaptation der Kurve des Tagessehens entspricht: Die grösste Differenz zwischen der Helligkeitskurve des Tages- und Dämmerungssehens ist nicht im Violett, sondern im Blau zu beobachten. Ebenfalls verständlich ist die Lage der Weisskurve zwischen 552 und 507 mμ: Das Xenonlicht (6200° K) zeigt wesentlich stärkere Emission im kurzwelligen Spektrum als das Glühlampenlicht (etwa 2800° K), dessen Kurve etwa zwischen 605 und 552 mμ liegen dürfte (vgl. KOHLRAUSCH, 1931). Gegenüber früheren Untersuchungen (KOHLRAUSCH, 1922; GRANIT, 1942; DONNER und RUSHTON, 1959) wird hier eine Zweiteilung der Dunkeladaptationskurve nicht nur für langwellige Lichtreize, sondern für sämtliche Wellenlängen beobachtet. Das von den genannten Autoren beobachtete Fehlen des Knicks in der Dunkeladaptationskurve bei kurzwelligen Lichtreizen ist möglicherweise als Folge ungenügender Helladaptation anzusehen, da der Knick in der Adaptationskurve umso früher erscheint, je schwächer die Helladaptation ist (vgl. Abb. 2).

Sehr konstant ist nach stärkerer Helladaptation der in Abb. 4 zwischen der fünfzehnten und fünfzigsten Minute der Dunkeladaptation deutliche 2,4-fache Anstieg der Reizschwelle

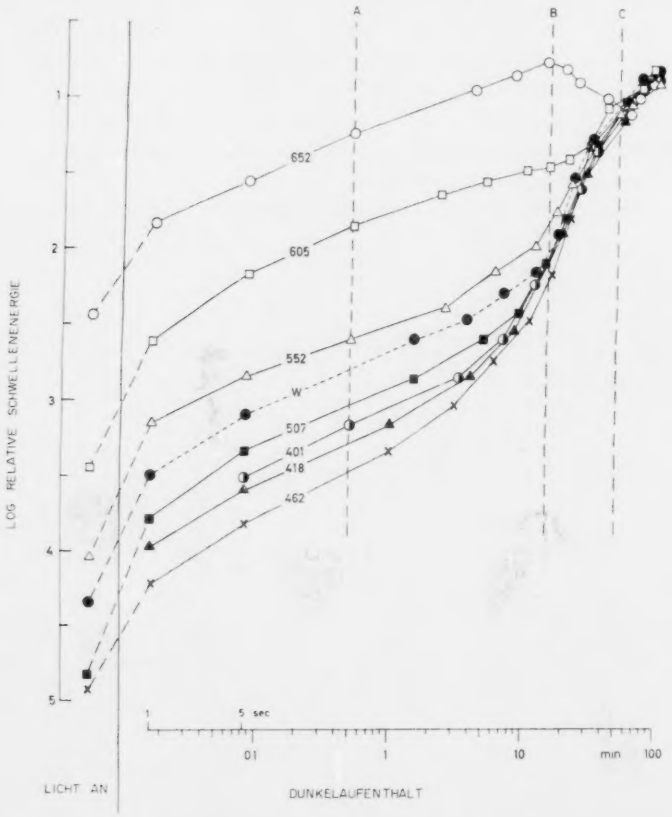

ABB. 4. Dunkeladaptationskurven eines Froschauges für Lichtreize verschiedener Wellenlänge (401–652 mμ) und für weisses Xenon-Licht (W). Ordinate: Relative Energie für eine Antwort im Elektroretinogramm von 20 μV, Null Ordinate = relative Energie nach 12 Stunden Dunkeladaptation für die verschiedenen Wellenlängen und für weisses Licht. Abszisse: Adaptationsdauer.

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für 652 mμ, während die Schwelle für 462 mμ gleichzeitig auf 1/16 abnimmt. Der Anstieg der Rotschwelle fällt damit zeitlich mit der zweiten Phase der Dunkeladaptation für kurzwellige Lichtreize zusammen. Ein ähnlicher Anstieg der Rotschwelle während Dunkeladaptation wurde von BARLOW, FITZHUGH und KUFFLER (1957) bei Ableitung von einzelnen Retina-Ganglienzellen der Katze registriert, jedoch nicht weiter beachtet.

Bei Kenntnis der spektralen Dunkelempfindlichkeitskurve lässt sich aus Abb. 4 die Veränderung der Helligkeitskurve zu jedem beliebigen Zeitpunkt der Dunkeladaptation unmittelbar ablesen. Nach 30 Sek (Senkrechte A) und 50 Min Dunkeladaptation (Senkrechte C) erhält man die Helligkeitskurven des Tages- bzw. Dämmerungssehens, und nach 15 Min Dunkeladaptation (Senkrechte B) eine breite "mesopische" Helligkeitskurve mit photopischen und skotopischen Anteilen. Somit bleibt im langwelligen Spektrum während Dunkeladaptation relativ lange die Tagesempfindlichkeit bestimmend, während im kurzwelligen Spektrum früh eine gesteigerte Blausensitivität auftritt, die mit fortschreitender Dunkeladaptation auch auf den blau-grünen Bereich übergreift (vgl. GRANIT, 1942; DONNER und RUSHTON, 1959; AUERBACH, 1960). Der Übergang der Helligkeitskurve des Tages- zum Dämmerungssehen wird nach stärkerer Helladaptation erst durch Verminderung der Rotsensitivität vollständig.

(4) *Das Verhalten der Reizschwelle während Helladaptation*

Hierbei wird entweder die *zeitliche* Veränderung der Reizschwelle während einer konstanten adaptiven Beleuchtung bestimmt (dI/dt) oder die Änderung der Reizschwelle in Abhängigkeit von der *Stärke* der adaptiven Beleuchtung (Unterschiedsschwelle dI/I).

A. Die zeitliche Veränderung der Reizschwelle während Helladaptation. Bei der in Abb. 1 dargestellten Veränderung der Reizschwelle einer voll dunkeladaptierten Netzhaut bei Helladaptation mit $1{,}3 \cdot 10^4$ Trolands zeigt sich für etwa 1 Sek vollständige Unerregbarkeit der Netzhaut für Reize beliebiger Stärke. Als Ursache dieser Erscheinung ist maximale Entladungsfrequenz sämtlicher lichtaktivierter Neurone anzunehmen (RIGGS und GRAHAM, 1940). Wenige Sekunden später ist jedoch ein Elektroretinogramm wieder auslösbar, somit auch die Messung von Reizschwellen möglich. Hierzu wurde nach entsprechenden Vorversuchen jene Reizintensität festgestellt, die zu verschiedenen Zeiten der Helladaptation (5 Sek, 15 Sek, 1 Min usw.) eine elektrische Antwort von 20 μV auslöste (Abb. 1, offene Symbole). Dabei wird zwischen der fünften Sekunde und zwanzigsten Minute der Helladaptation eine 32-fache Senkung der Reizschwelle mit einem Halbwert bei 30 Sek festgestellt. Über eine ähnliche, jedoch wesentlich geringere Senkung der Reizschwelle während Helladaptation wurde beim Menschen berichtet (BAKER, 1955). Die demgegenüber beim Frosch um mehr als das 10-fache gesteigerte Schwellenveränderung lässt an besondere Verhältnisse denken, wie an die bei einigen Wirbeltieren durch Licht ausgelöste Wanderung des Netzhautpigmentes. Um diese Annahme zu prüfen, wurde bei einer Reihe dunkeladaptierter Frösche 0,5 mg Adrenalin in den Lymphsack injiziert, wodurch eine Pigmentwanderung ausgelöst wird (GARTEN, 1907); anschliessend wurde erneut die Änderung der Reizschwelle bei Helladaptation untersucht. Dabei ergab sich bei gleicher Beleuchtung statt einer 32-fachen nurmehr eine 2-4-fache Senkung der Reizschwelle. Falls durch Adrenalin eine ebenso vollständige Pigmentwanderung wie durch Helladaptation bewirkt wird, würde die Verschiebung der Pigmentgranula etwa einer Erhöhung der Reizschwelle um das 8-16-fache entsprechen.

B. Die Veränderung der Reizschwelle in Abhängigkeit von der adaptiven Beleuchtung. Hierbei wird zunächst für eine vollständig dunkeladaptierte Netzhaut das Verhältnis

zwischen Amplitude der *b*-Welle und Intensität der Testreize bestimmt (Abb. 5, gefüllte Kreise und D). Sodann wird die Netzhaut mit dem Adaptationsstrahl an eine Beleuchtungsstärke adaptiert, die im dunkeladaptierten Zustand eine soeben messbare Antwort im Elektroretinogramm auslöst. Nach einigen Minuten (zur Herstellung eines Adaptations-Gleichgewichts) wird während dieser Helladaptation wiederum die Amplituden-Intensitätskurve der *b*-Welle bestimmt (Abb. 5, Punkte und Linie 1). Der Abstand der Kurven D und 1 auf der Abszisse entspricht dann der Änderung der Reizschwelle zwischen Dunkeladaptation (D) und schwacher Helladaptation (1). In gleicher Weise wird das Verhältnis zwischen Amplitude der *b*-Welle und Intensität der Testreize für verschiedene Wellenlängen

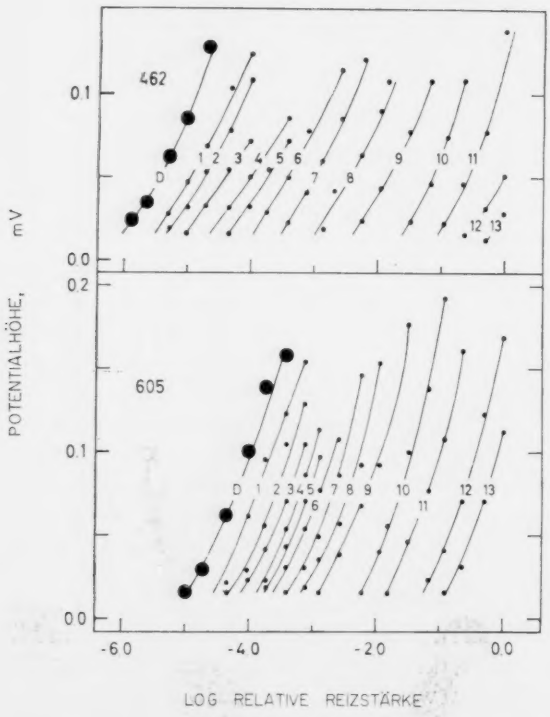

ABB. 5. Amplituden der *b*-Welle im Frosch-Elektroretinogramm (Ordinate) gegen Intensität der Testreize (Abszisse). Erste Messung bei Dunkeladaptation (D), dann während stufenweise gesteigerter Beleuchtung (1–13). Die jeweils folgende Beleuchtung ist etwa 4-mal stärker als die vorangehende. Testreize 462 mμ (oben), 605 mμ (unten). Dauer der Testreize 40 msec.

(462 mμ–oben, 605 mμ–unten) und für weitere adaptive Beleuchtungen gemessen, wobei durch Entfernung von Neutralfiltern aus dem Adaptationsstrahl die nachfolgende Beleuchtung jeweils etwa das 4-fache der vorangehenden beträgt (Punkte mit Linien 1–13).

Mit zunehmender adaptiver Beleuchtung erkennt man zunächst einen engen, dann weiteren, und schliesslich wieder etwas engeren Abstand der Amplituden-Intensitätskurven der *b*-Welle (Abb. 5). Entsprechend ergibt sich bei Aufzeichnung der Reizschwellen in Abhängigkeit von der adaptiven Beleuchtung ein angenähert *S*-förmiger Verlauf (Abb. 6). Dabei erhöht sich die Reizschwelle für weisse Testreize bei Steigerung der Beleuchtung von

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10^1 auf 10^5 der Dunkelschwelle nur auf das $10^{1,8}$-fache, bei Steigerung der Beleuchtung von 10^5 auf 10^8 der Dunkelschwelle dagegen auf das $10^{2,8}$-fache. Für den gesamten, hier geprüften adaptiv wirksamen Beleuchtungsbereich von 1 : $10^{7,25}$ beläuft sich die Änderung der Reizschwelle auf 1 : $10^{4,7}$. Unterschiedliche Werte ergeben sich bei Prüfung mit monochromatischem Licht, wobei sich für 462 mμ ein Verhältnis von 1 : $10^{5,5}$, für 605 mμ ein solches von 1 : $10^{3,6}$ ergibt (Abb. 6). Infolge der Purkinjé-Verschiebung ist die relative Änderung der Reizschwelle bei zunehmender adaptiver Beleuchtung somit für Blau wesentlich grösser als für Orange. Lediglich bei sehr schwacher Helladaptation entsprechen die für 462 und 605 mμ gemessenen relativen Schwellen jenen im dunkeladaptierten Zustand, während bei der höchsten, hier geprüften retinalen Beleuchtung die Netzhaut für 605 mμ etwa 70-mal empfindlicher ist als für 462 mμ.

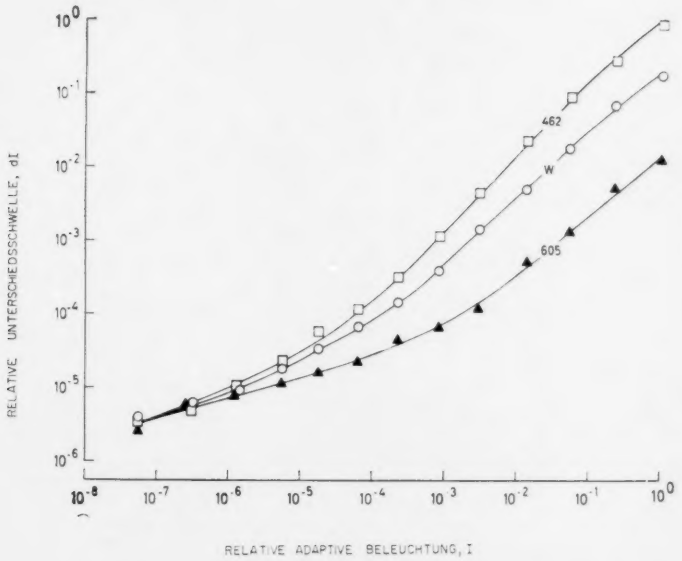

ABB. 6. Veränderung der Reizschwelle (Unterschiedsschwelle dI) der Froschnetzhaut bei verschiedener adaptiver Beleuchtung (I). Auswertung des Versuches von Abb. 5. Testreize: weiss (Kreise), 462 mμ (Quadrate), 605 mμ (Dreiecke).

(5) *Die Spektralsensitivität bei verschiedener adaptiver Beleuchtung*

Bei Ausschaltung räumlicher Summation durch Reizung sehr kleiner Bezirke der menschlichen Fovea und Netzhautperipherie fanden ARDEN und WEALE (1954) annähernd gleiche Empfindlichkeit für Stäbchen und Zapfen. Bei Reizung einer relativ grossen Area der Froschnetzhaut wie im vorliegenden Fall ergibt sich eine der Sehpurpurabsorption entsprechende Verteilung der Reizschwellen im Spektrum nur im dunkeladaptierten Zustand (Abb. 7, gefüllte Kreise). Helladaptation an ein soeben überschwelliges Licht (0,84 Trolands, gefüllte Quadrate) führt bereits zu einer deutlichen Steigerung der relativen Empfindlichkeit im langwelligen Spektrum, was auf eine relativ grosse Zahl rotempfindlicher Elemente in der Froschnetzhaut hinweist.

Messung der Spektralsensitivität während stufenweise gesteigerter adaptiver Beleuchtung

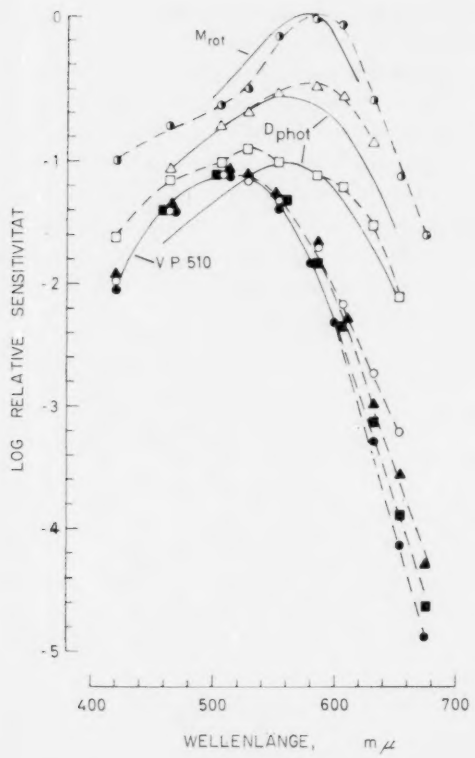

ABB. 7. Spektrale Augenempfindlichkeit des Frosches zwischen 418 und 673 mμ, erhalten durch Messung der für Einzelreiz-Elektroretinogramme konstanter Amplitude (20 μV) notwendigen Energie, bezogen auf ein Spektrum gleicher Quantenzahlen. Erste Messung nach 12 Stunden Dunkeladaptation (gefüllte Kreise), dann während stufenweise gesteigerter adaptiver Beleuchtung: 0,84 Trolands = gefüllte Quadrate; 13 Trolands = gefüllte Dreiecke; 105 Trolands = offene Kreise; 840 Trolands = offene Quadrate; 6600 Trolands = offene Dreiecke. 52 400 Trolands = Halbgefüllte Kreise. Ausgezogene Linien: LYTHGOE's (1937) Sehpurpurabsorption, für λ max 510 mμ umgezeichnet (V.P. 510); D_{phot} und M_{rot} = GRANIT's (1942) photopischer Dominator und Rotmodulator des Frosches.

zeigt deutlich die Inhomogenität des photopischen Dominators. Während bei 13 Trolands (gefüllte Dreiecke) und 105 Trolands (offene Kreise) die relative Rotempfindlichkeit ansteigt, wird bei 840 Trolands (offene Quadrate) die Sensitivitätskurve mehrgipflig mit einem Maximum im Grün und mit Nebengipfeln im Blau und Orange, um bei 6600 Trolands (offene Dreiecke) ein Maximum zwischen 584 und 605 mμ zu zeigen. Noch stärkere adaptive Beleuchtung (halbgefüllte Kreise) verengert die Empfindlichkeitskurve ohne Verschiebung des Maximums. Abgesehen von einer erhöhten Blausensitivität entspricht die bei 840 Trolands registrierte Kurve etwa Granits photopischem Dominator (D_{phot} ausgezogene Linie), während die bei 6600 Trolands erhaltene Kurve gegenüber der Dominatorkurve im Rot abweicht. Die bei der höchsten, hier zur Verfügung stehenden adaptiven Beleuchtung erhaltene Sensitivitätskurve zeigt einen ähnlichen Verlauf wie GRANIT's (1942) Rotmodulator (M_{rot}, ausgezogene Linie), doch ist die Kurve etwas zum langwelligen Spektrum verschoben.

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DISKUSSION

Der nach intensiver Helladaptation in der Dunkeladaptationskurve auftretende Knick wird als Übergang der photopischen (Tages-) zur skotopischen (Dämmerungs-) Aktivität der Netzhaut gedeutet, wobei jeweils das System mit geringerer Reizschwelle den Verlauf der Adaptationskurve bestimmt (KOHLRAUSCH, 1922, 1931). Dabei operieren nach Kohlrausch beide Netzhautsysteme unabhängig voneinander, während ELENIUS und HECK (1958) auf Grund der bei Stäbchenmonochromaten schnelleren Rückkehr der *b*-Welle für die zweite (skotopische) Phase der Dunkeladaptation eine aktive Depression durch den Tagesapparat annehmen. Beim Frosch ist eine verzögerte Dunkeladaptation erst nach einer retinalen Beleuchtung von 3300 Trolands und mehr festzustellen, während die Reizschwelle bei 20 Minuten Dunkeladaptation nach 210 Trolands kaum von den nach schwächerer Helladaptation erhaltenen Werten differiert. Dennoch ist nach 210 Trolands ein deutlicher Knick in der Dunkeladaptationskurve festzustellen (Abb. 2). Für eine Hemmung der Dunkeladaptation durch die Aktivierung des photopischen Systems ergibt sich somit in den gegenwärtigen Versuchen kein Anhalt. Dagegen ist eine wahrscheinlich nervöse Beeinflussung des Tagesapparates durch den Dämmerungsapparat deutlich nachweisbar, wie ältere Versuche (GRANIT und RIDDELL, 1934) und die hier demonstrierte Steigerung der Rotschwelle bei gleichzeitiger Zunahme der Blausensitivität während Dunkeladaptation zeigt.

Betrachtet man die bei Steigerung der adaptiven Beleuchtung gemessenen Veränderungen der Reizschwelle, so sieht man, dass die Empfindlichkeit in wesentlich geringerem Masse abnimmt, als dem Anstieg der adaptiven Beleuchtung entspricht. Dies gestattet dem Frosch, sich ohne entsprechenden Sensitivitätsverlust an einen weiten Bereich adaptiver Strahlung anzupassen, und bei natürlicher Pupille würde sich das Verhältnis noch weiter zu Gunsten der Reizschwelle verschieben, da die Pupille beim Frosch das auf die Netzhaut fallende Licht in einem Bereich von 1 : 10 kontrolliert (WEALE, 1956). Dieses Verhalten der Reizschwelle des Frosches bei Steigerung der adaptiven Beleuchtung steht in deutlichem Gegensatz zu jenem bei Dämmerungstieren wie Kaninchen und Ratten, deren Reizschwelle bei starrer Pupille während Helladaptation um den gleichen Betrag steigt, wie die adaptive Beleuchtung zunimmt (DODT, ECHTE und JESSEN, 1960). Indessen ist bei Säugetieren im Gegensatz zum Frosch eine Pigmentwanderung unbekannt (GARTEN, 1907), und nach den Versuchen mit Adrenalin entspricht diese Wanderung der Pigmentgranula während Helladaptation einer Verminderung der adaptiven Beleuchtung der Sinneszellen um mindestens das 10-fache. Bei Berücksichtigung der Pigmentwanderung ist die Veränderung der Reizschwelle für Testreize von 462 mμ tatsächlich etwa ebenso gross wie die Zunahme der adaptiven Beleuchtung ($dI/I=1$).

Der Zusammenhang zwischen den während Dunkel- und Helladaptation stattfindenden Veränderungen der Reizschwelle und den Konzentrationsänderungen der Photopigmente in den Sinneszellen wird zur Zeit diskutiert (WALD, 1957; RUSHTON, 1959). Übereinstimmend wird eine direkte Beziehung zwischen der Bleichung und Regeneration der Sehstoffe und den Veränderungen der Reizschwelle abgelehnt, da die Konzentrationsänderungen der Photopigmente um ein vielfaches kleiner sind als die Änderungen der Reizschwelle. Nach WALD (1957) variiert nicht die Reizschwelle, sondern deren Logarithmus mit der Pigmentkonzentration in den Sinneszellen, während RUSHTON *et al.* (1955) eine nicht-lineare Beziehung zwischen beiden Grössen beobachten.

Obwohl Froschaugen als besonders sehpurpurreich gelten, ist der Frosch wegen der bei Helladaptation zu beobachtenden Wanderung der Pigmentgranula kein günstiges Objekt zum Studium des Zusammenhanges zwischen Reizschwelle und Sehpurpurkonzentration,

falls die Konzentration der Photopigmente—wie in vorliegendem Falle—nicht direkt gemessen wird. Ausserdem enthält die Froschnetzhaut neben dem Sehpurpur möglicherweise noch andere Photopigmente. Dennoch ist ein Vergleich der hier vorliegenden Beobachtungen mit der von anderen Autoren gemessenen Photopigmentkonzentration bzw. Dem Bleichungszustand der Netzhaut des Frosches von Interesse. Von GRANIT, MUNSTERHJELM und ZEWI (1939) wurde beobachtet, dass die *b*-Welle im Elektroretinogramm während Dunkeladaptation erst nach Regeneration der Hälfte des Sehpurpurs ansteigt. Auf Grund der in der Einleitung genannten Bedenken ist die Methode des konstanten Reizes wenig geeignet, die Änderungen der Reizschwelle während Dunkeladaptation richtig wiederzugeben; immerhin dürfte der von GRANIT *et al.* (1939) beobachtete Anstieg der *b*-Welle dem Knick in der Adaptationskurve entsprechen. Nach SEGAL (1947) beginnt die Sehpurpurbleichung des Frosches *in vivo* bei 270 Trolands. Man kann daher annehmen, dass der Sehpurpur des Frosches bei der hier vorliegenden retinalen Beleuchtung von 52 400 Trolands vollständig gebleicht ist. Im Anschluss an diese Bleichung beträgt die Reizschwelle während Dunkeladaptation zum Zeitpunkt des Knicks etwa das 500-fache der Dunkelkontrolle (Abb. 2). Bis zu Zeitpunkt ist die Schwelle jedoch bereits um den Betrag der ersten Phase der Dunkeladaptation gefallen, was etwa der halben Adaptationsbreite entspricht und mit der von GRANIT *et al.* (1939) zur Zeit des Knicks beobachteten 50% igen Sehpurpurkonzentration übereinstimmt. Ein ähnliches Verhalten zwischen der Sehpurpurkonzentration während Dunkeladaptation und dem Anstieg der *b*-Welle wurde von den gleichen Autoren bei der Katze gefunden, und nach DODT und ELENIUS (1960) entspricht hier der Knick ebenfalls etwa der halben Adaptationsbreite.

Die Übereinstimmung zwischen der bei Dunkeladaptation zur Zeit des Knicks gemessenen 50% igen Sehpurpurkonzentration mit der 50% igen Rückkehr der Reizschwelle nach Bleichung entspricht der von WALD (1957) angenommenen Proportionalität zwischen Sehpurpurkonzentration und dem Logarithmus der Reizschwelle jedoch nur scheinbar. Bei der Ratte ist nach mässiger Helladaptation (10^4-mal Dunkelschwelle) eine ebenso grosse Steigerung der Reizschwelle festzustellen, ohne dass die Sehpurpurkonzentration wesentlich absinkt (DODT und ECHTE, 1961). Dennoch ist beim Frosch zwischen der retinalen Schwelle und der Sehpurpurkonzentration ein gewisser Zusammenhang erkennbar: Nach Helladaptation bis zu 210 Trolands benötigt die Reizschwelle bis zum 3-fachen der ursprünglichen Dunkelkontrolle etwa 20 Min, bei 270 Trolands beginnt nach SEGAL (1957) die Entfärbung der Netzhaut *in vivo* und nach Helladaptation mit 3300 Trolands und mehr ist die Dunkeladaptation auf 60 Min verlängert. Somit ist die Dauer des Dunkeladaptation kurz, solange keine oder nur geringe Bleichung des Sehpurpurs eintritt, dagegen lang, sobald der Sehpurpur in stärkerem Masse oder vollständig gebleicht ist.

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SUR UN EFFET D'INTERACTION BINOCULAIRE[1]

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Résumé—On décrit un effet de contraste binoculaire qui se produit pour des aires non-correspondantes des deux rétines: quand on présente un champ extrafovéal à l'un des yeux et qu'après quelque secondes on donne une stimulation très intense à une aire non-correspondante de la rétine de l'autre, la brillance du premier champ baisse notablement. Cet effet dépend de la luminance du champ éblouissant mais semble être presque indépendant de la localisation rétinienne du champ inhibiteur (pour des petites excentricités).

Abstract—A binocular contrast effect is described which involves interaction between non-corresponding areas of the two retinae: when one eye is presented with a peripheral field and then a non-corresponding peripheral area of the retina of the other eye is strongly illuminated, the observer reports a darkening of the first field. The effect cannot be ascribed to pupil contraction as it occurs with artificial pupils 2 mm in diameter. This binocular inhibition seems to be independent of the retinal location of the inhibiting stimulus (at least for small retinal eccentricities) and to depend on the relative intensity of illumination at the two eyes.

Zusammenfassung—Es wird ein binokulares kontrastphänomen geschrieben das sich ausdem zusammenwirkung nichtkorrespondierender Bereiche der Retinen erklären lässt: Bietet man dem einen Augen im Reizfeld extrafoveal dar und reizt dannen einen nichtkorrespondierenden Bereich der andern Auges mit hoher Intensität, so nimmt die Helligheit der ersten Reizfelds denklich ab. Diesen Effekt hängt von der Leuchtdichte der Blendfelds ab, scheint ab beim kleinen Excentricitäten von der Lage der inhibierenden Netzhautbereichs nahe zu unabhängig zu sein.

INTRODUCTION

L'EXISTENCE d'une interaction binoculaire est une question très controversée: les résultats des expériences sont contradictoires.

MUELLER-LIMMROTH (1954) a enregistré une variation de potentiel dans un oeil, produite par l'éclairement de l'autre, sur le cochon d'Inde; l'auteur a pu démontrer que la réponse électrique observée est due à un influx centrifuge provenant du corps genouillé. Mais GRANIT (1955) n'a trouvé aucun effet de ce genre sur le chat.

WIRTH (1951) a mesuré l'amplitude de l'onde *b* de l'électrorétinogramme d'un oeil, pour une stimulation donnée d'un des yeux, dans deux conditions: (1) l'autre oeil est stimulé en même temps que le premier; (2) l'autre oeil n'est pas stimulé. L'amplitude de l'onde *b* est plus petite dans le premier cas que dans le second. Mais UCHERMANN (1955) nie cet effet.

WRIGHT (1946), qui a mis au point la méthode de comparaison binoculaire pour les mesures photométriques et colorimétriques, a jugé que la variation de sensibilité d'un oeil produite par l'éclairement de l'autre est négligeable par rapport à la variation de sensibilité

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de l'oeil stimulé. Dès lors, tous ceux qui ont fait de la photométrie binoculaire ont admis que la sensibilité de l'oeil étalon est indépendante de la sensibilité de l'autre oeil (SCHOUTEN *et al.*, 1939; DIAMOND, 1953, 1955; LEIBOWITZ, 1953; HEINEMANN, 1955). IVANOFF (1947) nie tout effet d'interaction binoculaire quand les deux yeux sont éclairés à deux niveaux différents.

SOLÌS, AGUILAR et PLAZA (1953) ont mesuré le seuil différentiel d'un oeil tandis que l'autre voyait un champ uniforme beaucoup plus grand que le champ photométrique vu par le premier oeil. La valeur du seuil dépend du niveau d'éclairement du deuxième oeil, pour un niveau donné du champ photométrique. La valeur minimum est obtenue quand les deux champs ont le même éclairement. Ces résultats toutefois peuvent être dus à une contraction consensuelle de la pupille, étant donné que les mesures ont été faites avec des pupilles naturelles.

BOUMAN (1955) qui a conduit une recherche très complète à ce sujet, trouve des résultats un peu différents. Le seuil de contraste mesuré par un des yeux, pendant que l'aire correspondante de la rétine de l'autre est éclairée continuellement, ne diffère guère du seuil de contraste monoculaire, si les observations sont limitées aux intervalles de temps pendant lesquels le premier oeil n'est pas "dominé" par l'autre, par rivalité binoculaire. Si, au contraire, on mesure le seuil de contraste d'un oeil pendant un éclairement intermittent de l'autre, à des instants différemment décalés par rapport aux périodes de lumière, on trouve que le seuil est très haut au début et à la fin de chaque période de lumière, tandis qu'il baisse au milieu des intervalles de lumière ou d'obscurité. Bouman pense que cette interaction binoculaire est due à un mécanisme central, qui pourrait être en relation avec l'attention ou d'autres activités fluctuantes du cerveau.

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L'argument de la présente recherche nous a été suggéré par une observation occasionnelle faite au cours d'une expérience de photométrie binoculaire: nous avions observé que, si on presente un champ extrafovéal à l'un des yeux et si après quelques secondes on donne une stimulation très intense à une aire *non-correspondante* de la rétine de l'autre, la brillance du premier champ baisse notablement. Cet effet de contraste binoculaire est très semblable à l'effet de contraste monoculaire qui se produirait si les deux champs étaient vus par le même oeil. L'effet n'est pas dû à une contraction de la pupille, parce qu'il se produit même avec des pupilles artificielles de 2 mm de diamètre. Comme nous n'avons trouvé dans la litérature aucune description d'un effet de contraste binoculaire pour des aires non-correspondantes des deux rétines, nous nous sommes proposés de rechercher: (1) si l'effet était perçu par d'autres observateurs, qui n'étaient pas au courant du but de l'expérience, (2) s'il y avait un effet semblable à la fin de la présentation du champ éblouissant, (3) si l'effet était influencé par la distance apparente entre les deux champs pour une luminance donnée de l'autre, comme il arrive pour le contraste monoculaire.

Comme l'effet dont nous venons de parler est une variation *temporelle* de la brillance sujective, dont on s'aperçoit à la présentation du champ éblouissant, et comme on n'a pas la possibilité de comparer la brillance avant et après l'éblouissement avec une brillance étalon invariable, on ne peut "mesurer" l'effet de contraste qu'avec une méthode indirecte. Nous avons adopté une méthode utilisée par IVANOFF pour sa recherche sur l'effet d'éblouissement monoculaire (1947). Cette méthode consiste à faire augmenter d'une quantité réglable à volonté la luminance du champ qui subit l'effet de contraste, simultanément à la présentation du champ éblouissant. On peut trouver une valeur de la luminance additive telle que, au moment de la présentation du champ éblouissant, aucune variation de brillance ne se produit sur l'autre champ. Les mesures ont été faites par la méthode des stimuli constants.

METHODE EXPERIMENTALE

Le dispositif que nous avons employé permet de présenter à l'oeil gauche un champ carré, T (côté: 2°,3), éclairé par une lampe à incandescence et un point de fixation rouge, et à l'oeil droit un autre champ, I, ayant les même dimensions que T et un point de fixation rouge égal à celui présenté à l'oeil gauche. Les luminances des deux champs et leurs positions par

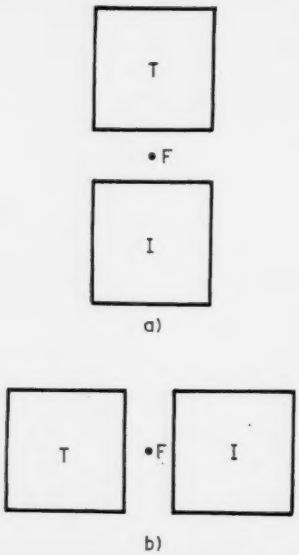

FIG. 1. Positions des champs T (vu par l'oeil gauche) et I (vu par l'oeil droit) en vision binoculaire, quand les points de fixation F sont fusionnés. Pour quelques observations les champs étaient dans la position a, pour d'autres dans la position b (voir le texte).

rapport aux points de fixation, peuvent être reglées par l'opérateur. Le point de fixation de l'oeil gauche se trouve près du milieu d'un côté de T et le point de fixation de l'oeil droit près du milieu du côté opposé de I, de manière que, en vision binoculaire, quand les deux points sont fusionnés, les deux champs se trouvent en deux régions du champ visuel opposées par rapport au point de fixation (Fig. 1).

Des obturateurs permettent de présenter l'un des champs indépendamment de l'autre; les points de fixation sont toujours visibles même lorsque les champs ne sont pas éclairés. L'obturateur qui commande la présentation du champ I, commande aussi, simultanément, l'éclairement additif de T. Les luminances de T et de I peuvent être variées par échelons de 0,1 unité logarithmique. La luminance additive de T peut être variée avec continuité par des "polaroids".

Toutes les observations ont été faites avec une pupille artificielle de 2 mm pour chaque oeil. Avant de commencer les observations, l'observateur est préadapté à l'obscurité pendant 10 min. Ensuite il arrange le dispositif binoculaire jusqu'à la fusion des points de fixation qu'il fixe pendant quelques minutes tandis que les champs T et I sont éclairés, pour adapter les deux aires rétiniennes aux niveaux correspondants. Chaque observation consistait en: présentation de T à l'instant t_0; présentation de I (et éventuellement éclairement additif de T) 2 sec après t_0; extinction des deux champs 4 sec après t_0. A la fin de chaque observation l'observateur doit dire s'il a vu une variation de brillance de T après présentation de I, et dans quel sens la brillance a varié.

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Les temps de présentation ont été choisis en prenant en considération que: un retard de 2 sec entre la présentation de T et celle de I est suffisant pour que la brillance subjective de T ait atteint un niveau constant; le champ T ne devrait pas disparaître à cause du "peripheral fading", puisque la latence du fading n'est pas inférieure à 4 sec pour les localisations rétiniennes des champs que nous avons employées (CLARKE, 1957).

L'intervalle entre deux observations successives n'était jamais inférieur à 5 sec, pour éviter les effets dus à l'éclairement périodique d'un oeil, qui ont été décrits par BOUMAN (1955).

RESULTATS

(*a*) *Recherche de l'Effet de Contraste sur Cinq Observateurs*

Le but de cette expérience était de prouver l'existence de l'effet de contraste binoculaire sur plusieurs observateurs. Les observations ont été faites par cinq sujets, dont quatre étaient entraînés en photométrie binoculaire (A.F.; T.R.; M.B.; P.L.), tandis que le cinquième était un sujet orthophorique qui n'avait jamais fait d'égalisation photométrique binoculaire (R.M.). Deux observateurs seulement (A.F.; T.R.) étaient au courant du but de la recherche.

Les points de fixation étaient situés à 0°,5 au-dessus du côté supérieur de I et à 0°,5 au-dessous du côté inférieur de T, respectivement. Après fusion, les deux champs étaient vus l'un au-dessous de l'autre, avec une séparation de 1°, sur un fond noir (Fig. 1a).

La luminance de I (L_t) était 300 nit, celle de T (L_t) 0,2 nit (1 nit=1 cd/m^2).

Dans quelques observations L_t restait constant lors de la présentation de I, c'est à dire qu'on ne donnait à T aucun éclairement additif (observations *a*); dans les autres observations, comme on a déjà dit, L_t a été augmenté d'une quantité ΔL_t, simultanément à la présentation de I (observations *b*). Les observations *a* et *b* se succédaient au hasard sans que l'observateur pût savoir ce qui se passait; il devait répondre "plus" ou "moins" selon qu'il avait observé que le champ T devenait plus clair ou plus sombre après la presentation de I; la réponse "égal" était admise pour les cas où l'observateur ne s'était aperçu d'aucune variation de la brillance de T. Les valeurs à donner à ΔL_t étaient choisies par un groupe d'observations préliminaires, de façon que les valeurs extrèmes donnent respectivement 5–10 per cent et 80–90 per cent de réponses "plus".

Pour prouver l'existence de l'effet de contraste binoculaire pour les cinq observateurs on n'a tenu compte que des observations *a*; les probabilités des réponse "moins" et "égal" obtenues sont données ci-dessous:

	obs.	A.F.	T.R.	P.L.	M.B.
Nombre total des observations *a*		100	100	116	70
Probabilité de réponse "moins"		0,98	0,99	0,85	0,84
Probabilité de réponse "égal"		0,02	0,01	0,07	0,09

Les résultats montrent que l'effet de contraste est perçu par les quatre observateurs dans la plupart des observations. Il faut toutefois remarquer que les observateurs P.L. et M.B. ont donné un certain nombre de réponses "plus".

Un observateur A.F. a fait aussi une série de vingt observations *a*, après instillation d'un mydriatique (sympamine en collyre) dans l'oeil gauche. Cet observateur n'a donné que des réponses "moins" et a remarqué que le noircissement observé sur T était aussi remarquable

que pendant les observations sans mydriatique. Ce fait nous a permis de confirmer que l'effet de contraste n'est pas dû à une contraction consensuelle de la pupille de l'oeil gauche.

L'observateur R.M. a donné 33 per cent de réponses "plus", 27 per cent de réponses "égal", sur un total de 412 observations *a*. Ce fait parait indiquer que cet observateur ne perçoit aucun effet de contraste binoculaire dans les conditions de l'expérience décrite. Toutefois, le fait que les réponses sont réparties en parties presque égales entre les trois genres de réponses possibles, pourrait signifier que cet observateur donnait des réponses au hasard.

(*b*) *Effet de la Variation d'Excentricité du Champ Eblouissant*

On peut se demander si l'effet de contraste binoculaire est affecté par la localisation rétinienne des deux stimuli maculaires. Pour répondre à cette question, des observations ont été faites par un observateur (T.R.) avec cinq excentricités différentes de I (distance entre le côté supérieur de I et le point de fixation: 0°,2; 0°,5; 1°,5; 2°,5; 3°,5) pour une excentricité constante de T (distance entre le point de fixation et le côté inferieur de T: 0°,5). Le nombre total des observations pour chaque excentricité de I est: cent observations *a*, cinquante observations *b* pour chacune des trois valeurs de la luminance additive de T, choisies précédemment. La luminance de T était 1 nit, celle de I 300 nit.

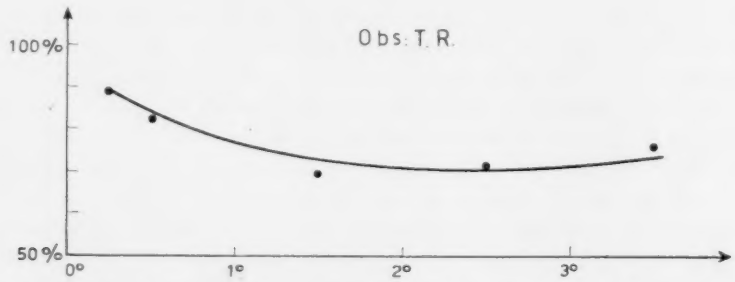

FIG. 2. Probabilité de réponse "moins" en fonction de l'excentricité du champ I ($L_t = 1$ nit; $L_t = 300$ nit).

Pour les observations *a* l'observateur n'a donné que des réponses "égal" ou "moins". Le nombre des réponses "moins" obtenues (observations *a*) pour les différentes positions de I est représenté sur la Fig. 2: la probabilité de percevoir l'effet de contraste binoculaire est legèrement plus haute quand la distance de I au point de fixation est inférieure à 1°, que pour des distances entre 1°,5 et 3°,5.

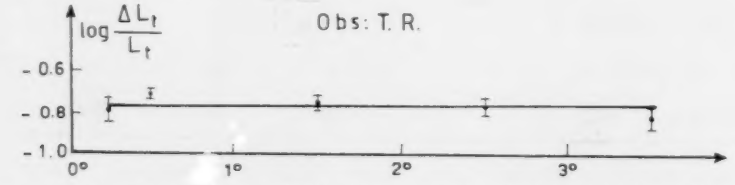

FIG. 3. Seuil relatif de luminance additive de T en fonction de l'excentricité de I ($L_t = 1$ nit; $L_t = 300$ nit).

A partir de la courbe de fréquence des réponses "plus" en fonction de la luminance additive de T (observations *b*) on a calculé les valeurs ΔL_t de la luminance additive qui correspondent à 50 per cent de réponses "plus". Les résultats sont représentés sur la Fig. 3:

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en abscisses la distance de I au point de fixation, en ordonnées le logarithme du rapport $\Delta L_t/L_t$. Les valeurs de ce rapport sont à peu près constantes dans l'intervalle de luminances considéré.

A propos de la localisation rétinienne des deux champs monoculaires, il nous a paru intéressant de rechercher si l'effet de contraste binoculaire a lieu aussi quand les images des deux champs se trouvent l'une sur la partie droite d'une rétine et l'autre sur la partie gauche de l'autre, c'est à dire sur deux aires rétiniennes qui sont projetées séparément sur les deux hémisphères cérébraux droit et gauche. La position des deux champs était celle indiquée sur la Fig. 1b, avec une séparation de 0°,5 entre le point de fixation et le côté plus proche des champs. Les luminances étaient: $L_t=1$ nit, $L_i=300$ nit. Les observations ont été faites par un observateur (A.F.) qui a annoncé 67 per cent de réponses "moins" (observations *a*): la probabilité de percevoir l'effet de contraste est assez haute même dans ce cas. Des observations *a* avec les champs dans la position indiquée sur la Fig. 1a et avec les même luminances, ont donné 78 per cent de réponses "moins".

(*c*) *Effet de la Luminance des Champs*

Pour étudier l'effet de contraste binoculaire en fonction de la luminance du champ éblouissant, des observations ont été faites par un sujet (A.F.) avec cinq luminances différentes de I (700; 56; 6; 2,4; 1,3 nit) et pour une luminance constante de T (0,15 nit). Les champs étaient dans la position de la Fig. 1a, avec une séparation de 0°,5 du point de fixation. Pour les observations *a* on a obtenu 100 per cent de réponses "moins" pour toutes les valeurs de la luminance de I. Pour chaque valeur de la luminance L_i on a calculé la luminance additive ΔL_t qui corresponde à 50 per cent de réponses "plus"; les résultats sont représentés sur la Fig. 4 (en abscisses log L_i, en ordonnées log $(\Delta L_t/L_t)$. Ces résultats montrent que le seuil de la luminance additive de T augmente avec la luminance du champ éblouissant I.

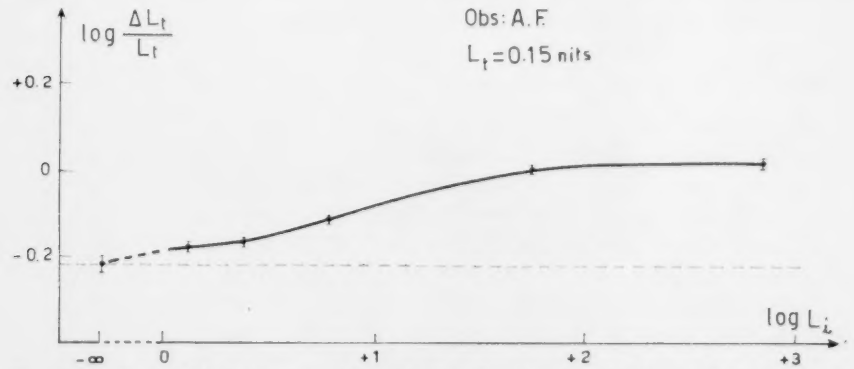

FIG. 4. Seuil relatif de luminance additive de T en fonction de la luminance de I, pour $L_t=$ 0,15 nit.

Il est intéressant de comparer ces résultats avec le seuil successif monoculaire mesuré par l'oeil gauche avec la même méthode employée pour les mesures binoculaires, mais sans présentation du champ éblouissant, c'est à dire pour $L_t=0$. (T était présenté pendant 2 sec, puis la luminance de T était soudainement augmentée d'une quantité variable; l'observateur devait répondre "plus" ou "égal" pour annoncer s'il s'était aperçu ou non de la variation de luminance.) Le seuil de la luminance additive avec le champ éblouissant est plus haut que

le seuil mesuré sans ce champ, même pour une luminance de I qui n'est que dix fois plus grande que la luminance de T.

Une autre série d'observations à été faite pour étudier l'effet de contraste binoculaire en fonction de la luminance de T. Les observations ont été exécutées par deux sujets (A.F., T.R.) avec une valeur constante pour la luminance de I (300 nit) et différentes luminances de T (2; 1; 0,5; 0,2; 0,15; 0,06 nit). Comme le seuil différentiel monoculaire est aussi une fonction de la luminance, les même sujets ont mesurés les seuils en l'absence du champ éblouissant, pour les valeurs de L_t indiquées.

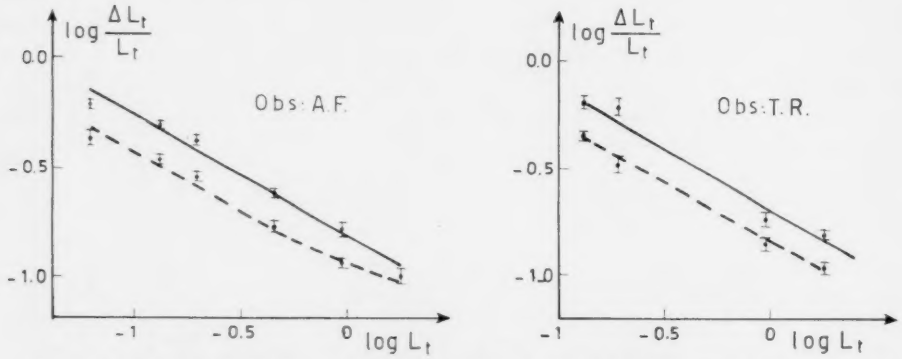

FIG. 5. Seuil relatif de luminance additive de T, en fonction de la luminance de T, pour deux observateurs, sans champs éblouissant (pointillé) et avec champ éblouissant (trait plein) de luminance 300 nit.

Les courbes en trait plein de la Fig. 5 représentent les résultats des mesures avec le champ éblouissant I, celles en pointillé les résultats des mesures monoculaires. La différence entre le logarithme des seuils sans et avec le champ éblouissant, se mantient à peu près constante, pour les différentes valeurs de L_t dans l'intervalle considéré.

(d) Latence de l'Effet de Contraste Binoculaire

Quelques uns des sujets ont observé qu'il y a un retard appréciable entre la présentation du champ éblouissant et le noircissement apparent de T. Nous n'avons pas encore fait de mesure de cette latence; nous avons seulement constaté que, si on augmente la luminance de T avec un retard de quelques centièmes de seconde sur la présentation de I, l'observateur ne perçoit aucune baisse sujective de brillance sur T. Si au contraire le retard est de quelques dixièmes de seconde, on voit d'abord le champ T devenir plus sombre et ensuite plus lumineux. Nous avons en programme une recherche plus complète à ce sujet.

On a mesuré le temps de perception de l'effet de contraste sur trois sujets (A.F.; T.R.; M.B.). Les observations étaient faites de la façon suivante: le champ I était présenté 2 sec après la présentation de T; les deux champs restaient éclairés ultérieurement pendant un intervalle dt variable et assez court, et enfin étaient éteints simultanément. Le sujet devait dire s'il avait réussi à percevoir une baisse de la brillance de T pendant l'intervalle dt, avant que les champs s'éteignent. Les valeurs de dt qui correspondent à 50 per cent de réponses positives pour les trois observateurs sont les suivantes: obs. T.R. 0,09 sec; obs. A.F. 0,06 sec; obs. M.B. 0,14 sec. Evidemment le temps de perception dépend beaucoup de l'observateur et on ne peut pas déduire de ces résultats une information utile pour l'interprétation du mécanisme responsable de l'effet de contraste binoculaire.

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(*e*) "*Off-effect*"

Pour rechercher s'il y a une variation de la brillance de T à l'extinction de I on a fait les observations suivantes (obs. A.F., T.R.): les deux champs étaient présentés en même temps; 2 sec après on éteignait I, tandis que T restait encore éclairé pendant 2 sec. Les luminances étaient: L_t=0,2 nit, L_t=300 nit, c'est à dire des valeurs pour lesquelles la probabilité de percevoir l'effet de contraste au début de la presentation de I est un, pour les deux observateurs. Ni l'un ni l'autre observateur n'a observé une variation de brillance de T simultanée ou successive à l'extinction de I.

Il faut remarquer que, s'il y avait une variation lente de sensibilité de l'oeil gauche à l'extinction du champ éblouissant, on ne pourrait pas la mettre en évidence avec notre méthode. Pour révéler une eventuelle variation lente de sensibilité il faudrait faire des mesures du seuil différentiel successif pour une luminance ajoutée au T à un temps variable avant ou après l'extinction de I.

DISCUSSION

L'effet de contraste binoculaire dont nous venons de parler démontre que la sensibilité d'un oeil dépend de la stimulation de l'autre, même quand les deux aires rétiniennes stimulées ne sont pas correspondantes. La variation de sensibilité a été prouvée: qualitativement, par une baisse de la brillance apparente du champ monoculaire qui subit l'inhibition; quantitativement, par l'accroissement du seuil différentiel successif, mesuré simultanément à la presentation du champ éblouissant. Nos observations ne nous permettent pas de savoir si la sensibilité de l'oeil qui subit l'inhibition varie pendant toute la durée de la stimulation de l'oeil inhibiteur, ou bien si la variation de la sensibilité est limitée à un intervalle de temps, autour du début de la stimulation de l'oeil inhibiteur. Comme on a dit dans l'introduction, pour des aires correspondantes BOUMAN (1955) prouve qu'aucune variation de sensibilité differentielle n'a lieu pendant une stimulation constante des deux yeux, tandis qu'une diminution de sensibilité a lieu au début et à la fin de chaque présentation du champ éblouissant lors d'une présentation périodique de celui-ci.

Pour ce qui concerne le mécanisme qui produit cet effet, deux interprétations sont possibles: l'action inhibitive peut se produire à un des derniers niveaux de la perception, c'est à dire que le mécanisme de l'inhibition serait purement central; ou bien l'inhibition agit directement sur la rétine par un influx centrifuge délivré à un niveau supérieur. Puisque l'effet se produit pour des aires rétiniennes non-correspondantes, et même pour deux hemisphères rétiniens opposés, c'est peut être plus probable qu'il s'agit d'une inhibition purement centrale. Si l'inhibition est transmise à la rétine, alors il faut supposer que la stimulation d'une aire limitée de la retine d'un oeil puisse faire délivrer un influx centrifuge capable de reduire la sensibilité d'une aire bien plus étendue de la rétine de l'autre oeil.

Une fois que l'existence d'un effet de contraste binoculaire a été prouvée, effet qui ne peut pas être expliqué par un mécanisme purement rétinien, on peut se demander, comme beaucoup d'auteurs l'on fait, s'il y a aussi une composante centrale du contraste monoculaire. BAUMGARDT et SÉGAL (1947), par exemple, ont décrit un métacontraste binoculaire (pour des aires correspondantes) avec des constantes de temps beaucoup plus grandes que celles du contraste monoculaire. Ces auteurs admettent, par conséquence, l'existence d'une composante centrale de l'inhibition. Il faut remarquer que cette composante doit avoir une importance secondaire par rapport à la composante rétinienne de l'inhibition, dans le cas où le contraste varie avec la distance entre les champs. Mais, selon des mesures de LEIBOWITZ, MOTE et THURLOW (1953), le contraste rétinien ne subit aucune variation

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sensible à cause d'une variation de la distance du champ inhibiteur, quand celui-ci devient extrafovéal.

Nous terminerons par la remarque que l'effet de contraste binoculaire peut avoir des conséquences pratiques désagréables: une source éblouissante située au dehors du champ visuel d'un oeil, mais visible par l'autre, peut produire une diminution de sensibilité de l'oeil qui n'est pas directement éclairé, et cet effet va s'ajouter à la baisse de visibilité par diminution d'éclairement rétinien produite par la contraction consensuelle de la pupille.

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ECOLOGICAL OPTICS

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Abstract—An attempt is made to define the potential stimulus for an ocular system, that is, the special features of the electromagnetic flux in the transparent medium of the environment (water or air) which make it possible for animals to see things. Insects and mollusks, as well as vertebrates, have developed organs for this purpose during the course of evolution.

It is suggested that, whereas the study of physics is concerned with radiant light, the study of vision is concerned with ambient light, and that the latter should be measured in different terms and conceived in a different way from that which classical optics has so far assumed.

A stationary optic array is characterized by different intensities in different directions, and it is proposed that the ray be conceived as the locus of a transition of intensity instead of the locus of an absolute intensity. The set of all transitions in an array is its structure. The task of ecological optics will be to specify and measure the structure of stationary arrays, both the fine structure and the overall pattern. It will also be necessary to describe the transformations of structure of moving optic arrays.

The central problem of vision is taken to be the question of how the ocular equipment of animals registers the information about the environment which is carried by these variables and invariants of structure.

Résumé—On tente de définir le stimulus potentiel d'un système oculaire, c'est à dire les caractères spéciaux du flux électromagnétique dans le milieu transparent environnant (eau ou air) qui permettent aux animaux de voir les objets. Les insectes et mollusques, tout comme les vertébrés, ont développé des organes dans ce but au cours de l'évolution.

On suggère que, tandis que l'étude physique de la lumière la considère comme un rayonnement, celle de la vision la considère comme une ambiance, ce qui conduit à la concevoir et à la mesurer autrement que l'optique classique ne l'a fait jusqu'ici.

Un arrangement optique stationnaire est caractérisé par des intensités différentes dans diverses directions, et on propose de concevoir le rayon comme un lieu de changement d'intensité plutôt qu'un lieu d'intensité absolue. L'ensemble de toutes ces transitions dans un arrangement constitue sa structure. La tâche de l'optique écologique est de spécifier et de mesurer la structure des arrangements stationnaires, à la fois la structure fine et le schéma général. Il sera nécessaire aussi de décrire les transformations de structure dans des arrangements optiques en mouvement.

Le problème central de la vision semble la question de savoir comment l'équipement oculaire des animaux enregistre l'information sur l'environnement qui est fournie par ces éléments variables et invariants de la structure.

Zusammenfassung—Es wird versucht den Reiz, verursacht durch die spezifischen Eigenschaften des elektromagnetischen Flusses in einem umgebenden transparenten Medium (Wasser oder Luft), zu definieren, der es Tieren ermöglicht Dinge zu sehen. Im Laufe ihrer Entwicklung haben Insekten, Mollusken und Wierbeltiere Organe für diesen Zweck entwickelt.

Es wird vorgeschlagen an Stelle der physikalischen Untersuchungen über Licht, das von einer Punktlichtquelle auf einer Oberfläche ausgeht, die Untersuchungen über das Sehen mit Licht, das an einem Beobachtungspunkt im Medium zusammenkommt, anzustellen, und letzteres soll in einer von den bisherigen Annahmen der klassischen Optik abweichenden Art gemessen und sich vorgestellt werden.

Eine stationäre optische Anordnung ist durch verschiedenen Intensitäten in

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verschiedenen Richtungen charakterisiert und es wird vorgeschlagen, dass der Strahl als ein Ort eines Intensitätsübergangs anstatt eines Ortes absoluter Intensitätsübergangs anstatt eines Ortes absoluter Intensität betrachtet wird. Die Menge aller Übergänge einer Anordnung ist ihre Struktur. Die Aufgabe der ökologischen Optik wird es sein, die Fein- und Grobstruktur einer Anordnung anzugeben und zu messen. Es wird auch notwendig sein, die Transformation der Struktur bei bewegten optischen Anordnungen anzugeben.

Als zentrales Problem des Sehens wird die Frage gesehen, wie das Augensystem von Tieren die Information über die Umgebung, die durch die Varianten und Invarianten ihrer Struktur gekennzeichnet ist, registrieren.

THE OVERALL problem of vision is that of understanding those activities of men and animals which depend on the stimulation of their eyes. This includes not only problems like the discrimination of wavelength, intensity, and flicker, but also the study of surface, form, space and motion. For vision in this general sense of the term, classical optics, taken straight, is not an adequate basis. It creates troublesome puzzles and contradictions of theory. Perhaps students of vision should reconsider some of the fundamental assumptions about light which they have borrowed from physics.

A large part of physical optics is admittedly not appropriate for the study of vision, nor relevant to it. The theory of the design of optical instruments is of great importance, but it cannot be taken over and applied to the eye. For an eye is *not* an optical instrument, despite all the textbook comparisons. An eye is logically prior to any optical instrument, and incommensurable with it. An instrument is something which is intended, in the last analysis, to be used by an eye.

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We are accustomed to say that the stimulus for an eye is light, and in truth it has long been known that the stimulus for the kind of photoreceptor found in a lower animal is the light falling on it. The effective limits of wavelength and intensity have been measured. Accordingly it is easy to assume that the stimulus for the eye of a higher animal is the light falling on a mosaic of photoreceptors. But this analogy is misleading, for the characteristic activity of an eye is not that of a simple photoreceptor. An eye proper, including both the chambered organ of the vertebrates or the higher mollusks and the compound organ of the higher insects, enables its possessor to respond not only to light but also to the things from which light is reflected. Just what does stimulate such an eye? What is it naturally adapted to register? To what is it sensitive, considered as an organ instead of a mosaic of cells? "Light" is much too simple an answer. A better answer is needed, and one might begin by suggesting that an eye registers *ambient* light. The remainder of this paper will be an effort to elaborate this answer.

The use of the term "ambient" suggests the light that surrounds an individual on all sides. This is part of what is intended. But I wish to refer more particularly to the light which arrives from all directions at a position in space and which does so whether or not an individual is stationed at that position. If this light has different intensities in different directions, instead of the same intensity in all directions, I propose to call it an *optic array*. It is an array because the variation of intensities makes an *arrangement*.

In our world, which is primarily composed of air and surfaces, the air transmits light and the surfaces reflect it. They reflect light diffusely, not regularly, since mirrors are rare in nature. Moreover, they reflect in multiple fashion, from one surface to another and to yet another. The outcome of diffuse reflection and multiple reflection is a reverberating flux of light in the transmitting medium. When analyzed in terms of rays, such a reverberating flux consists of a dense intersecting network made up of pencils of rays. A pencil can be defined

as a cluster of lines meeting at a common point, and there will be two types of pencil, divergent and convergent. The divergent pencils are cases of light radiating from a point source on a surface; the convergent pencils are cases of light coming to a point of observation in the medium. The former might be called "radiant" and the latter "ambient". Each of the convergent pencils of light in an ordinary illuminated environment is an optic array.

The radiant pencils issuing from point-sources can be properly treated as physical energy and measured as such. But I suspect that the convergent pencils to a point of observation should be treated as *potentially stimulating* energy, not energy as such, and that they cannot be measured in the same way. The ray of ambient light, I will suggest, should be conceived as different from the ray of radiant light.

I cannot discover that the facts about ambient light have ever been fully recognized in optics, or in any allied discipline. They are more or less recognized in books on perspective, or perspective geometry. But this discipline came to a halt many years ago, having achieved a satisfactory set of rules for the making of pictures by artists and architects. The special rules applied to a *picture plane* and a *station point*. We should not allow these special rules of pictorial perspective to take the place of a general study of environmental perspective. The viewing of pictures is by no means the same problem as the viewing of the environment, but many writers have tended to confuse them.

The above set of facts is also more or less implicit in the technology of making images on viewing screens. The concept of *projection* uses the idea of a pencil of rays intersecting in a point, thereby analyzing the correspondence between an object and its image. Taken abstractly, the concept is the basis of projective geometry. But neither of these disciplines is directly relevant to the problem of vision. The term "projection" is unfortunate when applied to the light stimulating an eye since this event is more like introjection than projection. The practice of illuminating engineering likewise depends on the same set of fundamental facts, but it does not seem to have been formulated or exploited.

These considerations have convinced me that psychologists, physiologists and others concerned with vision should try to define a special branch of optics appropriate for their problems. I suggest that it be called *ecological optics*. It would be concerned strictly with light in its capacity to stimulate eyes. It would be physics, in a sense, because it deals with a form of physical energy. It would be ecological because it deals with the relation of this energy to a concrete environment which reflects light. I venture to propose a set of assumptions for ecological optics. They are useful in putting a foundation under the kind of visual experiments I have been doing. They may also prove useful to other experimenters but, even if not, they should at least provoke a re-examination of optical theory.

1. THE CONCEPT OF AN OPTIC ARRAY

The primary assumption is that the natural stimulus for the ocular equipment of the higher animals is what I have called an *optic array*. An optic array is the light converging to any position in the transparent medium of an illuminated environment insofar as it has different intensities in different directions. Differences in spectral composition may accompany the differences of intensity. Geometrically speaking, it is a pencil of *rays* converging to a point, the rays taking their origin from textured surfaces, and the point being the nodal point of an eye. We have already noted that rays may diverge from a reflecting point (or a luminous point) as well as converge to a point of observation but that a divergent pencil of rays is *not* an optic array. The essence of an optic array is that it has pattern or structure. The radiant pencil has no pattern.

It should be noted that if the medium of the illuminated environment is not transparent, if it wholly scatters the reverberating flux of light by reason of fog or dust, then no optic array can exist in that medium. Likewise no optic array can occur in complete darkness.

The Optic Array as a Stimulus

The above assumption may astonish some readers. An optic array is extended and enduring whereas the word "stimulus" suggests something punctate and momentary, like a pinprick. An optic array is external to the eye. It cannot act all at once. Above all, it violates the accepted belief that the retinal image is the stimulus. I am suggesting, however, that we re-examine the meaning of that term.

It is just as reasonable to suppose that a sense organ can be stimulated as to suppose that a single receptor-cell can be stimulated. So can a whole sensory system. Each has its own level or order of stimulation. An optic array is the proper stimulus for an ocular system. A retinal image is the proper stimulus for a retina, considered by itself. But we should not be preoccupied with it to the exclusion of other facts. A single eye admits only a *sector* of a complete optic array at any one time. But the ocular equipment of an active animal, as we shall note, can respond by one method or another to a complete spherical array. As we know, the first responses of a man to an optic array, if he is awake, are to focus, fixate, modulate its intensity, and above all *explore* it. The optic array is a *potential* stimulus. It is also a *global* stimulus rather than a *punctate* stimulus.

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Retinal stimulation and ocular stimulation have to be distinguished. One is inside the eye and the other outside. The steady application of an image to the human retina (by artificially "stabilizing" it) results in a wholly ineffective stimulus after a short time. But the steady application of an optic array to an eye, which is the natural condition, does not so result. The movements of the eye prevent it. Another proof of the distinction is the fact that both the compound eye of an insect and the camera-eye of a vertebrate can respond to an optic array, but that only the latter kind of an eye has a retinal image. The optic array is an essential feature of all vision; the retinal image only of vision in some animals.

In speaking of the optical stimulus one must distinguish between simultaneous action and successive action. For the kind of animal with a panoramic ocular system, with eyes on each side of the head, the whole optic array is a simultaneous stimulus, or nearly the whole of it. For animals like ourselves with forward-pointing eyes the optic array is physically present at the station-point but it has to be sampled in successive overlapping sectors. In short, a single eye in a given posture registers no more than half of an array but an ocular system is constructed either to register a whole array or to explore it. By either mechanism animals react to their surroundings. How the nervous system integrates the successive patterns of retinal input and makes them equivalent to a simultaneous pattern of input is, of course, a question.

The eyes are different in different species of animals but the natural stimulus for all animals is the optic array, that is, the *differences* in ambient light. The latter is the "adequate" stimulus for vision. It is the circumstance under which eyes developed during the millions of years of evolution. Artificial or "inadequate" stimuli of all sorts can be applied to eyes, of course, and this is how we study vision experimentally. Some of these are quite unlike the natural stimulus; some are like it. At one extreme, electrical current can be used to excite the retina. If the subject will fixate on verbal command, a measured beam of light can be thrown into the eye and presumptively on the retina. Or a picture can be put in front of an eye, and this can reproduce part of a natural optic array—a sort of window opening

on an environment other than the present one. This is a favorite method of psychologists. The possibilities of controlling light rays to one or both eyes are endless. Psychophysical experiments on vision have unlimited possibilities. But in constructing optical devices we should remember, I think, the kind of stimuli that eyes are equipped to register.

The Set of Optic Arrays at Differing Station Points

Animals with eyes move about in the environment. The optic array at one position will, in general, be different from that in any other position. That is, its pattern will be different. It will be so by virtue of the laws of parallax and perspective. No two "perspectives" of the world are ever exactly the same. The change from one stationary optic array to another is itself assumed to be a kind of stimulus for an ocular system. All eyes, including the compound type, are known to be sensitive to "motion" and this assumption is, therefore, reasonable. One might even suppose that the optic array at a moving viewpoint is just as much an effective stimulus as the array at a stationary viewpoint (GIBSON, 1958).

The set of changes from one to another optic array in a given environment and the set of moving optic arrays come to the same thing. They are equivalent to the *complete* set of all stationary arrays in that environment. This is an abstract notion, more familiar to geometers than to students of vision. Nevertheless it is a useful concept. It defines the permanent possibilities of optical stimulation for the environment in question. It is potential stimulation, of course, and the actual or effective stimuli for a particular animal or man will always fall short of it no matter how thoroughly he inspects his part of the world. The notion of an unlimited reservoir of potential stimuli for the eyes to explore is a very fruitful one for visual theory.

The change of pattern from one stationary optic array to another can be termed a transformation of pattern. For animals with a panoramic ocular system, the whole global transformation arising from a change of location is a simultaneously present potential stimulus. It probably serves as a controlling input for their locomotion. For animals like ourselves, with forward-pointing eyes, matters are more complicated. The whole transformation of the array during locomotion can be registered only by successive sampling, but the simultaneous mismatch of the two slightly different arrays at the two eyes can be picked up in front, and this sensitivity to binocular parallax is undoubtedly a compensating advantage.

2. THE CONTENT OF AN OPTIC ARRAY

An optic array was said to consist of "rays". But in ecological optics, I believe, a ray should not be conceived as a beam of light, not even as one which vanishes to a geometrical line, but as the transition between one beam, and the next. It is the locus of a change in light energy over the array. Considered in two dimensions, the array would consist not of spots or patches but of the boundaries between them. This means that if an optic array had no transitions along either meridian, if it were homogeneous with respect to energy and spectral composition, it would not be a stimulus for an eye and would not be an array at all. The energy of the ambient light could be measured by instruments but it would not stimulate an eye to its characteristic activity. There are many facts to support this inference.

The concept of a beam of light which becomes vanishingly thin but still retains a given intensity and spectral character is troublesome. Such a fiction may be useful for geometrical optics, and convenient for the tracing of rays through refracting media, but it cannot

stimulate an eye. A transition, however, *can* stimulate an eye. The rays of ecological optics, being the loci of transitions, are not infinitely dense as they are supposed to be in pure geometry. Ecological optics does not have to be concerned with the problem of waves or particles nor with the laws of refraction, reflection, and diffraction. It is primarily concerned with margins, borders, contrasts, ratios, differences, and textures in the array.

The stimulating properties of an array thus depend on what is loosely called its structure. It will have both microstructure and macrostructure. An ordinary daylight array will have a fine structure at the level of seconds of arc, a coarse structure at the level of minutes, and a gross structure at the level of degrees. Outdoors, the upper half of the array will come from the sky and the lower from the earth. The fine structure corresponds to the rays coming from very small or very distant things; the gross structure corresponds to those coming from very large or very near things. The levels of structure exist whether or not an attentive eye is in a position to pick them up. Within what limits they are registered is another question. It depends on what kind of eyes the animal has, not on ecological optics.

We must not confuse optical structure with material structure. The texture of focusable light is not the same as the texture of the surface which reflected it, although the one tends to *correspond* to the other in important respects. The precise geometrical relation between the layout of opaque substances in space and the layout of luminous transitions in an optic array has to be determined by ecological optics.

There is a great advantage in defining the optical stimulus in terms of the transitions between spots or patches of light, not the spots or patches themselves. It encourages the use of relational magnitudes in visual experiments instead of the absolute magnitudes borrowed from physics. Physiologists used to assume that the elementary stimulus for vision was a narrow beam of light, measured for wavelength and intensity, that could be applied to a single receptor, and then to suppose that the whole of vision could be derived from knowledge of these elementary stimuli and their effects. It seems to me that this program has failed. It would be better to start from the fact that an optic array as a stimulus is independent of the intensity of light over a wide range of intensities, that is, degrees of illumination. From noon to sunset the *contrasts* are the same. Only as light energy, and only when taken piecemeal, is the optic array different from noon to sunset. This hypothesis seems to show disrespect for the labors of photometry and radiometry. I do not mean to be glib about the measurement of light. I only wish to suggest that there are profound difficulties in all present efforts to do so in a way that is relevant to an eye. We do see the difference between noon and sunset, to be sure, and our eyes still have some function as photoreceptors, but this is not their *characteristic* function.

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3. THE STIMULUS VARIABLES IN AN OPTIC ARRAY

The essential stimulus variables in "light" have, since Newton, been taken to be wavelength and intensity, or amount of energy. These can be measured in fundamental physical units. Hue is in psychophysical correspondence to wavelength, and brightness to energy. When saturation is included, corresponding to wavelength "purity" or some such measure, one gets the three supposedly basic dimensions of sensory experience. A beam of light can vary in these three physical ways and, correspondingly, a patch of color in experience can vary in three ways. Vision is then supposed to be based on color-sensations. The formula is simple and is tied to simple physical measurement. The trouble with it is that, however amended and supplemented, it does not fit all the facts, not even all the facts of color vision.

Ecological optics would assume that the essential stimulus variables for vision are *not* to be found in a beam of light and are *not* wavelength and amount of energy. Instead, the stimulus variables depend on the optic array, and must be discovered by analyzing its structure. Variables of structure or pattern, to be sure, cannot so easily be tied to the fundamental measures of physics. They seem inexact. Nevertheless if the old theory is inadequate, a beginning must be made on a new one. If "color" does not account for vision, let us see if "pattern" will do so, and perhaps then discover that color phenomena will fall into line. Or, putting it in another way, perhaps we cannot understand how the retina works unless we understand how the eye works.

The transitions in a natural optic array are primarily transitions of intensity. These depend on the layout, the chemical and structural composition, and the illumination of the solids, liquids, and gases of the environment. That is, they depend on the edges, corners, and other irregularities of reflecting surfaces. The intensity transitions are usually accompanied by spectral transitions (changes in the wavelength distribution relative to the spectrum of the illumination), but these are secondary. The fundamental variables of an optic array would then be ones like the following:

(a) Abruptness of transition, or what is loosely called "sharpness" of the boundary. A penumbra is at one extreme and an edge is at the other. How to measure this variable is still a question.

(b) Amount of transition. It seems likely that this variable should be measured as a ratio or fraction of the adjacent intensities, not as the absolute difference between them.

(c) Shape of the boundary, e.g. rectilinear, curved, or pointed.

(d) Closure of the boundary or non-closure.

(e) Density of transitions, or number per unit angle of the array.

(f) Change in the density of transitions; also the rate of change of density. The latter is the "gradient" of density of texture.

(g) Motion of one boundary relative to others; or motion of each boundary relative to all the others. The latter might be called a "transformation". There can also be gradients of motion.

(h) Presence or absence of transitions within a closed boundary of the array.

This list might be extended indefinitely. It consists of "significant" variables (of which more later). They have all been isolated experimentally and shown to be effective stimuli. But they are only the ones I happen to have studied, and there are many other potential stimuli in an optic array.

4. THE INFORMATION CARRIED BY STIMULUS VARIABLES IN AN OPTIC ARRAY

When defined as above, the variables of an optic array may *carry information* about the environment from which the light comes. This is a central hypothesis for ecological optics. By "carry information", I mean only that certain variables in an array, especially a moving array, will correspond to certain properties of edges, surfaces, things, places, events, animals, and the like—in short to environmental facts. They will not, of course, replicate but only specify such facts.

This hypothesis is perfectly capable of being investigated, and the extent to which it is true or false can be determined. The difficulty has been that no discipline acknowledges the responsibility of doing so—of finding the connections between optical stimuli and their natural sources. The problem falls between ecology, optics, physiology and psychology.

There has been plenty of speculative theorizing about the so-called cues for perception but no empirical study of whether a cue is in fact a clue to its object. The late EGON BRUNSWIK called for a study of the "ecological validity" of cues (1956) but few have heeded him. However, he believed that the only relations that could be found between "proximal" stimuli and "distal" objects were statistical probabilities, and this made the problem seem overwhelmingly difficult. I cannot believe that it is so. The notion of an optic array puts the problem on a geometrical basis, not a statistical one, although an element of probability no doubt remains.

There are almost certainly laws by which some variables in the optic array specify some environmental facts. They need to be investigated. Here are some tentative ones to start with:

(a) A sharply bounded sector of the optic array specifies an object in the world; a penumbra specifies a shadow in the world.

(b) A textured patch of the array specifies an obstructing surface in the world; a homogeneous patch specifies air. This is "surface quality" vs. "film quality".

(c) The kind of texture in a patch of the array specifies the kind of substance composing the surface—water, sand, grass, fire.

(d) A rectilinear boundary in the array specifies a straight edge in the world. Angles specify angles, and curves specify curves although, of course, the shape of an object is not specified by its form in the array.

(e) A gradient of density of the *same kind* of texture in the array specifies the direction of recession of a continuous surface.

(f) A transformation of the pattern and texture of the whole array specifies a change of station point.

(g) A transformation of a textured and bounded patch of the array, in isolation, specifies a displacement of an object in the world.

There are surely also complements and corollaries of such laws which will tell us what optical variables do *not* specify environmental facts. For example, optical size does not specify the physical size of an object. But magnification specifies the coming closer of an object and minification the opposite with considerable reliability. The intensity of a patch in the array does not specify the reflectance of a surface in the world. But relative intensities over the whole array might specify the relative reflectances of the whole layout of surfaces. If the stimuli, once naïvely thought to provide information about the environment, turn out not to do so others may be discovered which do. There is no reason to conclude that knowledge of the world is impossible because "light" is empty of information.

Invariant Properties under Transformation of an Array

It was noted earlier that the optic array at one position is different from that in another, and that waking animals continually move about. As slight a change of viewpoint as $2\frac{1}{2}$ inches horizontally yields a change in the structure of the array—one that we are used to calling a "disparity" where retinal images are concerned. Consider the change of form and texture for any change of station point. Only some properties of the array change, not all of them. There are *variant* properties of such an array and *invariant* properties. Some "variables" are altered, others are constant. The invariant variables, as they might be called, have not been specified and listed, but they can be, and this is another task for ecological optics.

From projective geometry we know that when a form undergoes a perspective trans-

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formation some features are altered and others not. The same rule holds for the overall structure of an optic array.

The reason why invariants need to be isolated and studied is that they are potentially stimuli. Variants and invariants need to be distinguished. In the past we have assumed that an altered pattern at the eye is simply a different stimulus for the eye. This is not true for an unaltered property. It remains constant and is therefore the *same* stimulus. The unaltered property provides a possible basis for the impression of a constant object or a rigid surface (GIBSON, 1957). On this theory, the variants in an optic array specify motions of objects or of the individual; the invariants specify the permanent characteristics of the layout of the environment. Here is a radical departure from previous theorizing.

The classical explanation of the constancy of phenomenal objects with respect to shape and size has been to ascribe it to some higher mental process. None has been verified. Actually the problem is one of the constancy of the whole phenomenal environment, not merely of objects. As such it is part and parcel of the study of vision. The theory suggested explains the constancy of phenomenal space as well as that of objects in space. I omit color constancy, but I suspect it can be explained in a similar way by reference to invariants under change of illumination.

The problem of the control of locomotion by vision and the perception of moving objects has scarcely been touched on by psychologists. When the variant properties of a moving optic array have been separated from the invariant ones the necessary stimulus information will, I think, become evident (GIBSON, 1958).

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5. SOME IMPLICATIONS

These assumptions about light clarify some old puzzles and suggest many new experiments. The advantages that occur to me are as follows:

1. The concept of an optic array enables us to investigate vision without having to choose between sensation and perception. The known facts cannot be separated into these two categories, and the theoretical separation is becoming meaningless. For example, color-perception and surface-perception need to be studied in relation to one another.

2. The defining of higher orders of optical stimuli enables us to perform simple psychophysical experiments on qualities of experience previously called "perceptual". For example, gradients of optical texture can be used as stimuli for impressions of slant-depth.

3. The optic array permits the defining of *relational* magnitudes in the light entering an eye as well as *absolute* magnitudes of stimulus energy, and suggests new experiments in which pattern and sequence are systematically varied instead of frequency and intensity. For example, parameters of optical transformation can be used as stimuli.

4. The notion of an optic array which emanates from surfaces resolves the ancient theoretical puzzle of the "third dimension".

5. By providing a theory of the relation between the proximal stimulus and its distal source it promises to put the problems of size, shape, and color constancy on a new footing, to be treated as problems of vision instead of some little-understood kind of mental activity.

6. The optic array puts the retinal image in its proper place as one stage in the process of seeing in animals having chambered eyes.

7. It destroys the misleading analogy between the retinal image and a picture, while clarifying the relation between them. A picture is a human means of reproducing a part of a natural optic array.

8. It also enables us to bypass some of the long-standing paradoxes concerning the retinal image considered as a picture. For example, instead of worrying about double and single impressions from the two eyes we are led to consider information pickup in a conjugated binocular system.

9. The optic array requires us to consider the responses of the eye and the responses of the retina as each affects the other instead of treating them separately. The orienting and exploratory movements of the eyes developed in parallel with the structure of the retina.

10. Finally, if potentially stimulating light carries information about the environment, as ecological optics may demonstrate, the ancient problem of veridical perception is solved.

6. SUMMARY

I have made some tentative suggestions about how to further the study of vision by modifying our assumptions about light. They have been dignified by the term "ecological optics". An optic array was defined, and three main assumptions were made. They seem to be as follows:

1. There is a set of optic arrays in every habitable environment when it is illuminated.

2. Some correspondence exists between the structure of a local optic array and the structure of the local environment, also between the set of arrays and the whole environment.

3. The variables of structure in an array and a set of arrays are potential stimuli for an ocular system.

These hypotheses provide a novel basis for the study of the eyes. They suggest an assumption which common sense would like to accept but which students of vision have thought they had to reject, namely:

An ocular system is essentially a mechanism for registering the information about the environment in a set of optic arrays. It thereby makes possible the control of behavior with respect to the environment.

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FARNSWORTH HUE CIRCLES[1]

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Abstract—A tristimulus color mixing device is described which provides a continuously variable circle of colors, as on a color mixture diagram, in the manner of the Farnsworth Hue Circles. The device uses filters instead of pigment colors but the principle should be extended to spectrally pure stimuli.

Résumé—On décrit un appareil de mélange de couleurs à trois stimuli; cet appareil fournit un cercle de couleurs à variation continue, comme sur un diagramme chromatique, de la même manière que le cercle de couleurs de Farnsworth. Cet appareil utilise des filtres au lieu de pigments, mais son principe pourrait être étendu à des stimuli spectraux purs.

Zusammenfassung—Commander Farnsworth führte einen Farbtonkreis aus Munsell Farben als Test für Farbenblinde ein. Es wird ein nach diesem Prinzip gebautes Farbmischgerät beschrieben, das es unter Verwendung von drei Filtern ermöglicht einen kontinuierlichen Farbtonkreis aus drei Grundfarben im Mischungsdiagramm einzustellen. Dabei wird bei Änderung des Farbtons die Helligkeit immer konstant gehalten. Die Verwendung als Test für Farbenblindheit und zur Messung der Unterschiedsempfindlichkeit auf Farbton und Sättigung wird beschrieben.

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INTRODUCTION

ONE of Commander Farnsworth's many contributions to visual science was the use of a hue circle for testing for color blindness (1943). For this purpose, Commander Farnsworth selected Munsell papers which fell on a continuous ring on the color mixture diagram.

It occurred to the writer that Commander Farnsworth's basic idea could be utilized more effectively if instead of using Munsell colors one were to build a tristimulus color mixing device which would provide a continuous circle of colors on a color mixture diagram. I have attempted therefore to design and build such a device. Such a device ought to incorporate the following features:

1. There must be a continuous change in hue.
2. As the hue changes the luminance must be kept constant.
3. The circle of colors must be a perfect circle on a color mixture diagram in which the luminosity coefficients of the three primaries are all equal to unity.
4. The illuminant C must fall at the center of the circle.
5. Provision must be made for changing the colorimetric purity in order to produce hue circles of various diameters.

According to ADAM's (1942) analysis of the data for Munsell colors it should be possible to select three primaries which will yield rings surrounding illuminant C which represent approximately the lines of constant chroma. In the device which I have built the primaries are obtained by passing white light through colored filters. The finding of three suitable

[1] *Editor's Note*—This paper was scheduled for the Farnsworth Memorial Issue, but unfortunately it was not received in its final form in time.

filters has proved to be quite a problem and the difficulty encountered probably justifies abandoning the type of device which is about to be described and starting over with a new device utilizing spectrally pure stimuli. This would immediately solve the problems encountered in the selection of filters.

Nevertheless, the device which I have built demonstrates the principles involved as well as the unsolved problems and hence the device deserves to be described. This I am doing in the present paper. Later I expect to work on plans for a device utilizing the spectrally pure stimuli which will serve the same purpose as the instrument which has already been built.

A FILTER TYPE MIXING DEVICE FOR PRODUCING FARNSWORTH CIRCLES

The color mixing apparatus is shown in Fig. 1. The condenser lenses (E) and (F) produce an image of the filament (D) in the plane of the opal flashed glass (I), but the image of the filament is broken up by a piece of ground glass (H) which is placed a short distance in front of (I). This makes it possible to have the round aperture in the diaphragm (J) uniformly illuminated. Diaphragm (G) contains three rectangular apertures as shown in Fig. 2. The aperture (A) is covered by a blue filter, the aperture (B) by a green filter, and the aperture (C) by a red filter. The light therefore falling on the milk glass (I) is a mixture of three primaries.

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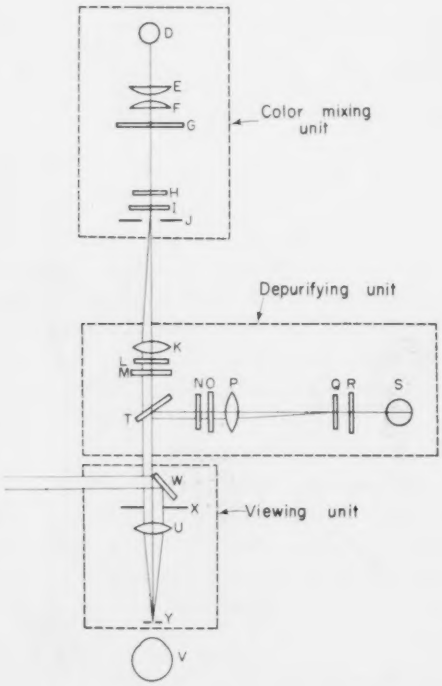

FIG. 1. A colorimeter for testing for color blindness. It can also be used for tracing lines of constant hue and constant chroma on a color mixture diagram and for measuring sensibility to chromaticity differences on normal subjects.

The proportions of the three primaries in the mixture can be controlled by varying the dimensions of the three apertures A, B and C. The amounts of the three primaries in the

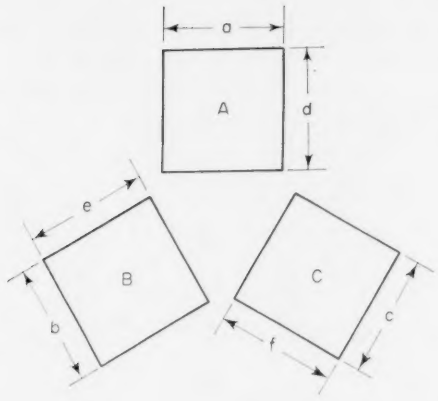

FIG. 2. Apertures in the diaphragm at (G) in Fig. 1.

mixture are proportional to the amounts of flux passing through the three apertures. The total flux through each aperture is given by the product of the area of the aperture and the illuminance in the plane of the aperture.

$$F_A = E_A\, da,\ F_B = E_B\, eb \text{ and } F_C = E_C\, fc.$$

The dimension a is constant but the dimensions b and c are adjusted by separate knobs so that

$$E_A\, a = E_B\, b = E_C\, c.$$

The dimensions d, e and f can then be adjusted simultaneously by a single knob in such a way that

$$d = \frac{a}{2}(1 + \sin\theta),$$

$$e = \frac{a}{2}[1 + \sin(\theta - 120^\circ)] \text{ and}$$

$$f = \frac{a}{2}[1 + \sin(\theta + 120^\circ)]$$

where θ represents the angular displacement of the control knob from its zero position. It follows therefore that

$$F_A + F_B + F_C = \frac{3}{2} E_A\, a^2$$

and is therefore equal to a constant.

s

The mechanism which produces simultaneously changes in d, e and f is illustrated in Fig. 3. The control knob turns the shaft (S) which drives the eccentric (M). The shaft (T) is synchronized with the shaft (S) and drives the eccentric (N). The two eccentrics (N) and (M) drive the diaphragm containing the triangular aperture which simultaneously manipulates the dimensions d, e and f.

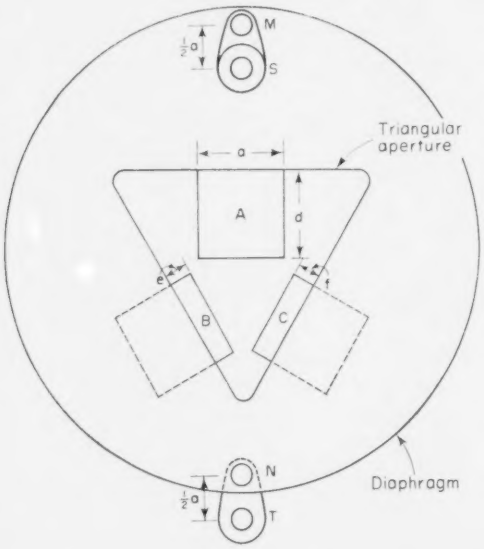

FIG. 3. Mechanism for varying the dimensions d, e and f.

Attention should be called to the fact that one can achieve the same end result by covering the three apertures (A), (B) and (C) in Fig. 1 with polaroid filters having axes oriented at 0°, 60° and 120°. Before allowing the light to pass through the three apertures covered with the three polaroid filters, it must be made to pass through a single piece of rotating polaroid which covers all three apertures. This piece of polaroid should be located between the condenser lens (F) and the diaphragm (G). By placing the rotating polaroid between the source and the fixed polaroid filters, each of the three beams of light falling on (I) is always polarized in the same direction.

The polaroid filters control the relative proportions of the three primaries in the mixture. The dimensions a, d, e and f may be kept equal but the dimensions (b) and (c) must be adjustable so that the maximum values for flux for (A), (B) and (C) are all equal to each other. With the fixed polaroids oriented at 0°, 60° and 120° the sum of their transmittance values must be equal to a constant and hence the total flux transmitted through the three apertures is equal to a constant. If we let θ represent the angular displacement of the axis of the rotating polaroid from the axis of the fixed polaroid covering aperture (A), the transmittances for the three apertures are as follows:

$$t_A = k \cos^2\theta,$$
$$t_B = k \cos^2(\theta + 60) \text{ and}$$
$$t_C = k \cos^2(\theta + 120).$$

The sum of the transmittances, therefore, is equal to a constant, 1·5 k.

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Regardless of whether one uses the triangular aperture or the polaroids to control the proportions of the three primaries in the mixture, one can use the same diagram (Fig. 4) to represent the tristimulus mixtures in a mixture diagram. If in a mixture diagram we plot the three primaries at the corners of an equilateral triangle after the manner of Maxwell the tristimulus mixtures will fall on a circle which is inscribed in the triangle. In such a mixture diagram the luminosity coefficients of the three primaries are equal.

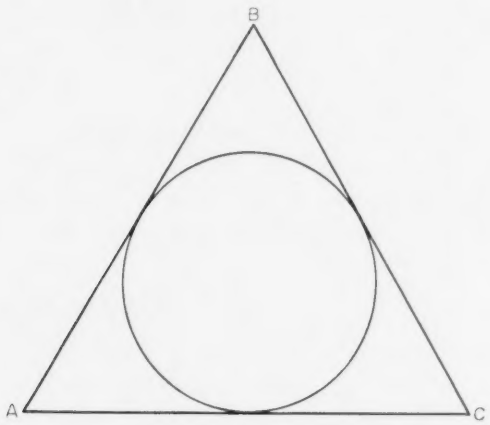

FIG. 4. Color mixture triangle showing the three primaries and the circle of colors generated by the color mixing unit.

The Depurifying Unit

The depurifying unit in Fig. 1 can be used to produce changes in colorimetric purity. The beam combiner (T) combines the beam from the color mixing device with a beam from a separate source (S) which illuminates the milk glass (R). This light is then converted by means of a filter (Q) to the C illuminant and after collimation by the lens (P) is passed through two polaroid filters (O) and (N). The light from the color mixture device is collimated by the lens (K) and passed through two polaroid filters (L) and (M). This beam is then combined with the beam from (S) by means of the beam combiner (T). (M) and (N) are fixed polaroids and (L) and (O) are rotating polaroids which are synchronized in such a way that as the flux from the color mixing device increases the flux from the sources decreases a complementary amount so that the total flux remains constant.

The Viewing Unit

The two beams combined at (T) provide illumination for the left half of the aperture at (X) which is viewed by the eye (V) through the lens (U) and the exit pupil (Y).

The right half of the aperture at (X) is covered by the first surface mirror (W) which is illuminated by the same kind of optical system as the left half of the aperture.

The aperture in the diaphragm at (X) may be a round hole giving a circular field divided into two parts by the edge of the mirror (W). However, the aperture may have any form, or may be replaced by two small apertures with a space between them. The front of the diaphragm is white and may be illuminated to give the colored matching stimuli any desired background.

TESTING FOR COLOR BLINDNESS

The apparatus described above can be used to test for color blindness in the same way as Farnsworth used his 100-Hue circle, except that continuous variations are available and this simplifies the procedure. One can set the two halves of the colorimetric field to give colors falling on the same hue circle and then vary the hue in one half to measure the just discriminable difference in chromaticity. A line, tangent to the hue circle at the point at which discrimination suffers impairment, indicates either a dichromatic confusion line or the direction in which the MacAdam ellipses are elongated for an anomalous trichromat.

The counterpart of Farnsworth's Dichotomous Test consists in locating the colors on opposite sides of the hue circle which are confused with each other.

MEASUREMENT OF SENSITIVITY TO CHROMATICITY DIFFERENCES

The device described above can also be used to map out lines of constant hue and constant saturation. Furthermore, it can be used to measure sensitivity to chromaticity differences along lines of constant dominant wavelength and along color circles concentric with white.

Acknowledgement—The device described above was discussed with Commander Farnsworth in Brussels in June 1958. At that time he expressed his interest and I regret that his untimely death occurred before the device could be put into use. Nevertheless, I am pleased to offer this paper as a tribute to him because it represents an extension of his own work. He was a friend to me and many others. His loss is deeply felt.

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INFLUENCE DU BRUIT SUR CERTAINES FONCTIONS VISUELLES

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Résumé—Un bruit complexe supérieur à 90 dB et agissant entre 5–10 min, n'altère ni l'acuité visuelle, ni le champ visuel, ni la composante physique du sens stéréoscopique.

Cependant on a observé que la perception pratique du relief était un peu perturbée. La vision des couleurs s'altérait aussi dans le sens de la protanomalie, à l'anomaloscope de Nagel.

Le sens morphoscopique nocturne, mesuré au scotoptomètre de Beyne, baisse fortement.

Cette diminution de la capacité de vision nocturne sous l'effet du bruit, semble due à une action centrale.

Zusammenfassung—Ein Geräusch über 90 dB mit ungleichmassigem Spektrum verursacht bei eine Reizzeit zwischen 5 und 10 Min Keine Veränderungen der Sehschärk, der Gesichtsfelds und der physikalischen Komponente des Stereoskopischen Sehens.

Es wurde jedoch beobachtet, dass das praktische Tiefensehen vermindet wurde. Ebenso veränderte sich das farbsehen im Sinn einer Protanomalie (übertruft mit dem Nagel'sehen Anomaloskop).

Das Nachtformsehen zeigte sich bei Untersuchung mit dem Skotoptometer nach Beyne stark herabgesetzt.

Diese beeinträchtigung der Nachsehvermögens unter dem Einfluss eines Geräusches hat wahrscheinlich zentrale Ursachen.

Abstract—A complex noise above 90 dB, heard during 5 to 10 min, did not cause any decrease in visual acuity, visual field, or the physical component of stereoscopic sense.

However, it was observed that the practical sense perception was disturbed. Colour perception was also modified with a trend to protanomaly as measured with the Nagel-anomaloscope.

The nocturnal morphoscopic sense, as measured with a scotoptometer of Beyne, is strongly impaired.

This decrease of night vision capacity under the influence of noise, seems due to a central action.

L'INFLUENCE du bruit sur l'organisme est bien connue des physiologistes mais peu d'études ont été consacrées à son action sur la vision.

Le système oculaire assure des missions différenciées: acuité visuelle, perception de l'espace, appréciation du relief, des couleurs, et exercice du sens morphoscopique nocturne.

S'il était établi que l'une ou l'autre de ces fonctions fût altérée par une ambiance sonore excessive, on conçoit les dangers qui pourraient apparaître dans certaines activités industrielles et les transports, où l'intégrité de la perception visuelle doit être parfaite et instantanée.

Nos expérimentations ont porté sur des sujets jeunes, ne présentant aucune altération fonctionnelle et organique de leur appareil oculaire. Leurs professions ne les avaient nullement habitués à une accoutumance au bruit.

Nous avons pris comme "bruit-test" celui fourni par le moteur d'une Vespa fonctionnant à l'arrêt sur le régime accélération de départ. Ce bruit complexe, relevé à 5 m dans l'axe de la source, a un spectre de fréquence étendu entre 50 et 5 000 Hz.

On peut distinguer dans ce spectre quatre parties:

1° Partie étendue entre 50 et 500 Hz, dont les fréquences ont chacune sensiblement la même intensité cependant que, dans le temps, elles varient de 5 à 8 dB en plus ou en moins de la valeur moyenne.

2° Partie étendue entre 500 et 2 500 Hz: chacune des fréquences présente le même type de variation par rapport à la valeur moyenne de l'intensité qui se situe à une valeur sensiblement plus élevée que dans la partie précédente.

3° Partie entre 2 500 et 3 000 Hz: l'intensité passe très rapidement par un maximum à la fréquence 3 000 Hz mais les variations de l'intensité, dans cette partie du spectre, sont du même type que dans les précédentes.

4° Partie entre 3 000 et 5 000 Hz: l'intensité de chacune des fréquences tombe rapidement sans subir de grosses variations dans le temps.

L'intensité sonore globale de ce spectre a varié, au cours de l'expérience, de 98 à 105 dB.

Enfin, la durée de l'exposition a été voisine de 5 min dans toutes nos investigations.

ACUITE VISUELLE

Trente sujets ont été, au préalable, examinés à l'optomètre de Beyne. Vingt-cinq d'entr'eux présentaient une acuité visuelle de 10/10 sans correction; par contre, les cinq derniers avaient un pouvoir séparateur inférieur à l'unité.

Aucune modification de la valeur de l'acuité n'a été décelée au cours de l'audition de ce bruit pendant 5 min, comme plusieurs minutes après la cessation du stimulus.

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CHAMP VISUEL

Vingt relevés du champ visuel ont été obtenus à l'aide de l'appareil de Goldmann aux index 5/4 et 3/1, permettant de constater que le schéma campimétrique restait normal, après 5 min d'exposition au "bruit-test", pour le blanc, le bleu et le vert. Par contre, nous avons décelé un rétrécissement marqué de 10°, en moyenne, pour la couleur rouge.

SENS DU RELIEF

L'appréciation du relief se fonde sur l'interprétation mentale de données optiques diverses parmi lesquelles figure la parallaxe stéréoscopique.

Nous avons donc utilisé, en premier lieu, les stéréogrammes de l'appareillage réalisé par la Société d'Optique et de Mécanique de Haute Précision. Ce test permet une mesure physique, strictement oculaire, de la valeur du sens du relief.

L'appareillage de Howard-Dolman fait, au contraire, intervenir l'analyse mentale de la détermination des distances. Il nécessite trois expériences pour chaque sujet à qui l'on demande de placer, sur le même plan qu'un tige fixe, une autre tige qu'il peut mouvoir à distance. La moyenne arithmétique des trois examens ne doit pas dépasser 30 mm d'erreur dans cette manoeuvre.

Les trente sujets examinés par ces deux procédés, sous la même influence sonore, ont répondu différemment à ces épreuves.

Aucune modification de la parallaxe stéréoscopique n'a été constatée.

Par contre, les valeurs moyennes, obtenues à l'aide de l'appareil de Howard-Dolman, peuvent être résumées ainsi:

Avant le bruit	14 mm
A la fin de la cinquième minute de bruit	28 mm
Un heure après la cessation du bruit	14,5 mm

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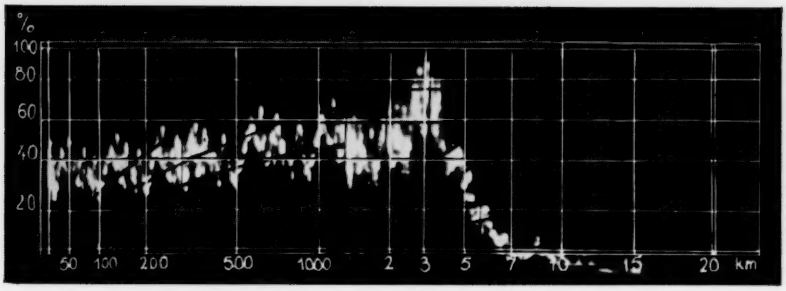

FIG. 1

[facing p. 270]

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La comparaison de ces différents résultats permet donc de constater que la composante physique du sens du relief n'est pas modifiée par le bruit. Par contre, l'appréciation réelle de la distance, qui fait entrer en jeu plusieurs éléments d'ordre psychologique (mémoire—raisonnement—intégration des différentes sensations périphériques), est légèrement perturbée. L'arrêt de l'émission sonore assure la récupération des capacités stéréoscopiques qui est effective après une heure.

VISION DES COULEURS

KRAVKOV (1936, 1939) avait constaté que l'influence du bruit sur la vision des couleurs se manifestait par une tendance à la protanomalie (déficience partielle pour le rouge).

Nous avons repris les expériences de cet auteur en utilisant, pour la détermination du sens coloré, la table d'Ishihara, l'anomaloscope de Nagel et la lanterne chromoptométrique de Beyne (feux simples présentés à 4 mètres pendant 1 ving-cinquième de seconde, sous une ouverture angulaire de 2 min; feux de confusion sous une ouverture plus grande, contemplés pendant 2 sec).

Dix sujets, présentant une vision des couleurs absolument normale, ont été soumis à l'influence du "bruit-test". A la fin de la cinquième minute, aucun d'entr'eux n'a commis d'erreurs à la lecture des tableaux d'Ishihara.

L'équation de Rayleigh s'est trouvée légèrement modifiée, sans qu'il y ait prédominance dans le sens d'une prota- ou d'une deutéranomalie (quotients extrêmes: 0,9 et 1,15).

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Par contre, la dénomination des feux colorés s'est trouvée perturbée dans 75 pour cent des cas (vert appelé blanc). Les feux de confusion ont été aussi souvent mal discernés.

Une heure après l'arrêt de l'émission sonore, la lecture était à nouveau entièrement normale.

Nous avons enfin étudié le comportement d'un deutéranope (type Nagel) et les erreurs qu'il commettait aux différents tests étaient plus appréciables après une exposition sonore.

En conséquence, si nous n'avons pas retrouvé la tendance à la protanomalie déterminée par KRAVKOV (1936, 1939), il paraît certain que le bruit apporte une perturbation légère dans la reconnaissance des feux colorés simples ou confusionnels. On y ajoutera le rétrécissement campimétrique que nous avons constaté pour le rouge dans l'étude des champs visuels.

VISION NOCTURNE

L'examen quantitatif de la vision nocturne a été précisé à l'aide du scotoptomètre de Beyne qui permet d'obtenir un seuil dont les limites normales varient de 0,07 à 0,12 bougie par mm^2. Il exprime alors la luminance la plus faible qui assure la détermination des formes d'un objet.

Les sujets ont été adaptés en chambre noire durant 25 min et soumis ensuite à un premier examen scotoptométrique qui a été renouvelé après 5 min de "bruit-test".

Nous avons constaté que la valeur moyenne du seuil, qui était de 0,09, est passée à 0,21. Cette différence est appréciable car la scotoptométrie nous a montré que la répétition des examens morphoscopiques, à quelques minutes d'intervalle, améliore généralement les valeurs obtenues. De plus, de récentes expérimentations ont démontré que la pluralité des stimuli, au cours des examens de vision nocturne, augmentait aussi le rendement de la performance.

Cette baisse de la capacité nocturne paraît donc assez nette: elle dépasse la valeur maximum admise pour un seuil normal. Ici encore, la récupération du chiffre initial a lieu une heure après la cessation du bruit.

CONCLUSIONS GENERALES

Cette étude analytique nous permet donc de constater que le bruit, que nous avons choisi et qui fait notamment partie de la gamme sonore d'une ambiance d'atelier, interfère sur l'activité visuelle.

L'étude discriminatoire du sens du relief, que nous avons pratiquée, confirme que les intensités sonores excessives agissent sur le cortex occipital et paraoccipital sans avoir d'influence directe sur l'oeil.

Cette notion semble trouver une confirmation dans l'étude des tracés électroencéphalographiques que nous avons fait pratiquer par Remond. Enregistrés au cours des examens scotoptométriques, pendant l'audition du bruit, ils ont montré une tendance à l'"endormissement" dans les premières minutes.

Par une technique encore plus fine d'enregistrement, on peut espérer déterminer les zones corticales où l'intégration est perturbée.

Sur le plan pratique, l'influence du bruit sur la vision peut engendrer des défaillances multiples.

Tout d'abord, celle de l'appréciation du relief que nous avons décelée et qui est susceptible d'altérer la précision du travail aussi bien chez l'ouvrier spécialiste qui manie continuellement ses instruments de travail que chez celui qui doit diriger de lourdes machines avec précision.

En outre, les modifications du sens chromatique, surtout pour le rouge, seront un facteur d'erreurs dans la comparaison des plages colorées qui est demandée dans bien des ateliers spécialisés.

Enfin, notons également la diminution de la capacité visuelle nocturne qui survient au cours du séjour dans le bruit. Elle affecte plus particulièrement les ouvriers des équipes de nuit travaillant dans des zones d'ombre où la discrimination des formes est encore diminuée par le bruit des machines. Sans oublier tous ceux qui, travaillant la nuit en basse lumière, sont obligés de conduire des engins bruyants, risquant ainsi de provoquer des accidents de transport et de la circulation.

D'autres recherches avec des intensités sonores différentes et prolongées apporteront sans doute des précisions complémentaires.

Pour terminer, nous devons insister sur la durée du temps de récupération qui paraît nettement plus importante que celle que l'on a coutume de constater dans la pathologie de l'oreille dans le bruit.

Mais, de toute façon, l'insonorisation des moteurs et machines outils doit être réalisée de telle façon que l'intensité des bruits complexes qu'ils émettent soit toujours au-dessous des valeurs entraînant une altération de l'acte visuel. Cette intensité-seuil doit se placer entre 85 et 95 dB globaux, ainsi que nous l'avons déterminé par ailleurs.

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BIOCHEMICAL CHANGES IN APHAKIA

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Abstract—The distribution of ascorbic acid in the normal eyes of cows and rabbits and in the normal, partially aphakic and completely aphakic eyes of guinea-pigs has been studied. By using one eye of each animal as a control it was shown that there were significant decreases in ascorbic acid concentrations in the vitreous in complete aphakia but that normal levels were restored by the presence of lens tissue. The high ascorbic acid content of the retina was not altered by the absence of the lens. The lower levels of ascorbic acid found in aphakia were attributed not to any lack of ability of ascorbic acid to enter the aphakic eye but to the failure to maintain ascorbic acid in the more stable reduced form. The vitreous was completely liquid in aphakic but not in partially aphakic eyes; high dietary intakes of ascorbic acid did not alter the physical state of the vitreous. The copper-catalysed oxidation of ascorbic acid is inhibited by the presence of vitreous humour; this protective effect can be removed by treating the vitreous with *p*-chloromercuribenzoic acid. Hydroxyproline and ascorbic acid have been determined in the retinae of various species. These results have been discussed in relationship to pathological changes in the eye.

Résumé—On étudie la distribution de l'acide ascorbique dans des yeux normaux de vaches et de lapins, et dans des yeux normaux, partiellement et totalement aphaques de cobayes. En utilisant comme témoin un oeil de chaque animal, on montre que la concentration dans le vitré de l'acide ascorbique diminue d'une façon significative pour l'oeil complètement aphaque, mais que la présence de tissu cristallinien rétablit la teneur normale. L'absence de cristallin n'altère pas la teneur élevée de la rétine en acide ascorbique. Les faibles valeurs d'acide ascorbique chez l'aphaque sont attribuées non pas à une impossibilité pour cet acide de pénétrer dans l'oeil, mais au défaut du maintien de cet acide sous sa forme réduite la plus stable. Le vitré était complètement liquide chez l'aphaque, mais non pas dans les yeux partiellement aphaques; de fortes ingestions d'acide ascorbique dans l'alimentation n'altèrent pas l'état physique du vitré. L'oxydation de l'acide ascorbique catalysée par le cuivre est inhibée par la présence d'humeur vitrée; cet effet protecteur est supprimé en traitant le vitré par de l'acide *p*-chloromercuribenzoïque. On a dosé l'hydroxyproline et l'acide ascorbique dans la rétine de diverses espèces. On discute ces résultats en relation avec les changements pathologiques dans l'oeil.

Zusammenfassung—Es wird die Verteilung von Ascorbinsäure untersucht, und zwar im normalen Auge von Kühen und Kaninchen, sowie im normalen, teilweise und gänzlich aphakischen Auge von Meerschweinchen. Ein Auge eines jeden Tieres wurde zur Kontrolle verwendet. So konnte gezeigt werden, dass die konzentration an Ascorbinsäure im Glaskörper bei völliger Aphakie beträchtlich absank, jedoch bei Fehlen der Linsengewebe wieder normale verhältnisse hergestellt wurden. Der hohe Gehalt an Ascorbinsäure in der Retina wurde bei Fehlen der Linse nicht verändert. Der geringe Gehalt an Ascorbinsäure, der sich bei Aphakie findet, wird nicht dadurch verusacht, dass dei Fähigkeit der Ascorbinsäure verlorenginge, in das aphakische Auge einzutreten, sondern die Ursache ist, dass die Ascorbinsäure nicht in der stabileren reduzierten Form erhalten werden kann. Der Glaskörper war vollständig flüssig im aphakischen, nicht aber im teilweise aphakischen Auge; grosse Dosen Ascorbinsäure änderten das physikalische Verhalten des Glaskörpers nicht. Die Kupfer-katalysierte Oxydation der Ascorbinsäure wird durch Glaskörperflüssigkeit gehemmt; dieser Schutzeffekt kann durch Behandlung

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des Glaskörpers mit *p*-Chloromercuribenzoesäure behoben werden. In den Retinae verschiedener Tierarten wurde der GehaltanHydroxyprolin- und Ascorbinsäure bestimmt. Diese Ergebnisse werden im Zusammenhang mit pathologischen Veränderungen im Auge diskutiert.

THE main object of this research was to study biochemical changes in aphakia that might explain the aetiology of primary retinal detachment. It is generally agreed that when retinal detachment occurs both the retina and the vitreous have undergone pathological changes (TENG and CHI, 1957). A large part of the vitreous is usually liquefied and contains strands, which by their traction at the site of vitreo-retinal adhesions, cause a break in the retina. The changes in the retina would appear to be concerned only with those elements of it which are necessary for structural integrity, since concomitant pathological changes to the nervous tissue do not take place, there being no deterioration in visual acuity immediately before a retinal detachment. In attempting to study these changes experimentally, advantage has been taken of the observation by SHAPLAND (1934) that in a series of twenty-two patients the average time of occurrence of retinal detachment was 24·6 years after the needling of the lens. These detachments of long-standing aphakia do not readily respond to surgery, owing to atrophy and the occurrence of secondary retinal breaks. SCHEPENS (1951) has suggested that detachment in aphakic eyes, following lens extraction for cataract, is part of a syndrome and removal of the lens is not the cause of the detachment but merely a precipitating agent; however, SHAPLAND (1934) has reported retinal detachments following discission of the lens in cases of myopia. It is not known what effect the discission of the lens plays in causing a detachment, but the long time that has elapsed since the cataract operation in Shapland's cases rules out purely mechanical causes such as vitreous loss or prolapse. It is possible that the removal of the lens has deranged the normal metabolic balance within the eye and so led to these pathological conditions. Therefore a study of the biochemical changes that take place in aphakia might give some insight into the biochemical lesions that eventually lead to retinal detachment.

FRIEDENWALD and PIERCE (1937) observed increased oxygen tension and FISCHER (1931) reported lowered lactic acid levels in the aqueous humour of aphakic eyes, due to oxygen consumption and lactic acid production by the lens no longer taking place. These results have never been disputed; on the other hand there has been much controversy over the observation that the level of ascorbic acid in the aqueous humour is lowered in aphakic eyes. MÜLLER and BUSCHKE (1934), BIETTI and CARTENI (1934), LANGHAM (1950) and BOYD (1955) have all reported lower levels, whereas FRANTA (1937), KINSEY (1950), KRONFELD (1952), PURCELL *et al.* (1954) and CHATTERJEE and GHOSH (1956) have come to the conclusion that there is no change in the level of ascorbic acid in aphakia.

Although ascorbic acid has been implicated in many different pathological conditions there is no doubt of its importance for the normal metabolism of the constituents of connective tissue, such as collagen fibres and mucopolysaccharides; for recent reviews see GOULD *et al.* (1960) and NEUBERGER (1960). As the vitreous body consists almost entirely of these substances and as the final pathological condition in the retina, a mechanical break, could well be described as a loss of tensile strength, it was decided to re-investigate the effect of aphakia, both total and partial, on ascorbic acid concentrations. The rate of synthesis and degradation of collagen varies with the site in the body. Although early reports stated that in tendon, collagen fibres were inert, more recent work has shown that a very slow metabolic turnover does in fact take place (GOULD *et al.*, 1960). A possible indication that the biochemical lesions might be due to derangement of collagen synthesis is given by the

length of time that elapses between the lens extraction and subsequent detachment. This hypothesis, based on the slow rate of collagen turnover, could account for changes in the vitreous, but it presupposes the presence of collagenous elements in the retina. Indirect evidence that the structural integrity of the retina depends upon collagen has been deduced from the observation that the injection of the enzyme collagenase into the vitreous body of the rabbit resulted in the complete disruption of the retina as well as of the vitreous and lens (PIRIE and VAN HEYNINGEN, 1956). It was therefore decided to estimate hydroxyproline as a measure of the collagen content of the retina.

EXPERIMENTAL

Animals

Male and female albino guinea-pigs were used, weighing approximately 220 g for needling and 300–450 g for intracapsular lens extraction. The animals were maintained on M.R.C. diet S.G.1 supplemented with cabbage, and water *ad lib.*

Surgery

Both eyes were treated with chloramphenicol 0·5 per cent and atropine sulphate 1·0 per cent, 18 hr and 1 hr prior to operation. The animals were anaesthetized by the intraperitoneal injection of sodium pentobarbitone, 0·2 gr/lb (28·6 mg/kg) body weight. Operations were performed on only one eye of each animal, the other being used as a control. The eye was anaesthetized with 2 per cent cocaine hydrochloride drops, 10 min before the operation. As far as possible these operations were carried out under aseptic conditions. Post-operatively the eyes were treated with chloramphenicol for several days. In some cases the eyes were treated with hydrocortisone 1·0 per cent, 8–10 days post-operatively in order to reduce corneal vascularization.

Three surgical techniques were used to render the eyes aphakic. The anterior surface of the lens capsule of seven young guinea-pigs was needled, but as regeneration occurred, another group of seven guinea-pigs was subjected to a more severe discission procedure. Even this did not result in the complete loss of the lens. In some cases regeneration occurred and in other cases the capsule healed with the formation of a small mishapen scarred lens. Needling as a method of producing aphakia in young guinea-pigs was therefore abandoned in favour of intracapsular extraction.

Intracapsular extraction. The lids were retracted by means of sutures. A superior limbal incision was made and extended from 10 to 2 o'clock. The lens was removed through the incision, which was then closed with a central suture and the lids closed by means of the retraction sutures. The post-operative complications of this method of lens extraction led us to adopt the following procedure, which was used for thirty-six guinea-pigs operated on in groups of six at weekly intervals. A small incision was made in the cornea at 12 o'clock with a scalpel and then extended vertically to 6 o'clock with de Wecker scissors. The lens was removed through the well-dilated pupil by applying gentle pressure. In most cases the lens was intact and there was no evidence of adherence of the vitreous to the posterior lens surface. In a few cases the lens capsule ruptured and incomplete extraction resulted. The lids were then sutured. No advantage resulted from suturing the corneal incision since healing began within a few hours. The lid sutures were removed on the seventh day if they had not previously broken.

Ascorbic acid supplementation. In order to study the effect of high ascorbic acid concentrations in the eye, the diet of six aphakic animals was supplemented from the fifth day after

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operation with 20 mg ascorbic acid per day, administered orally in 60 per cent sucrose. Ascorbic acid was not given 24 hr prior to sacrifice so that only true saturation values were obtained.

Preparation of tissues. The animals were killed approximately eight weeks after the operation when there were no apparent signs of inflammation. The guinea-pigs were anaesthetized with ether and death was caused by the removal of blood by heart puncture. Both eyes were enucleated, freed from extraneous tissue and weighed. Aqueous was collected with a glass capillary through a small incision in the cornea. The cornea was removed and blotted with Whatman No. 50 filter paper. The remaining aqueous was absorbed with wicks of filter paper, from the anterior chamber. The lens, if present, was freed from the zonular fibres with a lens expressor, separated from the vitreous and blotted. Four 5 mm incisions were made through the sclera, choroid and retina from the limbus posteriorly, so that the four joined quadrants could be laid flat on a watch-glass. The vitreous, iris, together with the ciliary body, the retina, choriod and sclera were then separated.

Determination of total ascorbic acid. This was based on the methods of ROE and KUETHER (1943), ROE *et al.* (1948), and SCHAFFERT and KINGSLEY (1955) with modifications to obtain the maximum sensitivity on a microscale. The tissues were ground with acid-washed sand, oxidized with bromine water, and deproteinized with 5 per cent metaphosphoric acid. The excess bromine was removed with 0·5 per cent stannous chloride in 5 per cent metaphosphoric acid. After centrifuging, 2 ml aliquots were incubated at 37° with 0·5 ml 2,4–dinitrophenylhydrazine, thiourea reagent, for 3 hr, cooled to 0° and 2·5 ml of 85 per cent sulphuric acid was added. After standing for 15 min, the absorption was measured at 510 mμ in a Unicam spectrophotometer, model 500. A linear calibration curve for pure ascorbic acid was obtained using the above method. An extinction of 0·112 was given for the equivalent of 1 μg of ascorbic acid/ml, in the final solution.

Determination of hydroxyproline in retina. The retinae from two bovine eyes (1·03 g) were homogenized with 30 ml 0·9 per cent sodium chloride and centrifuged at 12,000 r.p.m. for 15 min. The supernatant was discarded and the residue was washed four times by resuspending in 30 ml 0·9 per cent sodium chloride and centrifuging. The collagen was extracted from the residue by autoclaving twice with 3 ml water for 3 hr at 15 lb pressure. The extract was evaporated to dryness, dissolved in 1 ml 6*N* HCl and hydrolysed for 6 hr at 105° in a sealed tube. The hydroxyproline content was determined in the hydrolysate by the method of STEGEMANN (1958). Thirty-two rat retinae (0·35 g), ten guinea-pig retinae (0·18 g), three rabbit retinae (0·13 g) and the larger blood-vessels (0·21 g) from four bovine retinae were analysed by a similar procedure.

The stability of ascorbic acid on incubation. 1 ml of ascorbic acid (250 μg) was made up to a final volume of 3 ml by the addition of 1 ml McIlvaine's citric acid, phosphate buffer pH 6·7 and 1 ml bovine vitreous humour, aqueous or 10 per cent lens homogenate. A final concentration of 10^{-5}M glutathione or 10^{-6}M Cu^{++} was obtained by suitable additions to the buffer. After aerobic incubation for 1 hr at 37°, 2 ml 10 per cent metaphosphoric acid was added and the ascorbic acid estimated in 1 ml aliquots by the method of HUGHES (1956). In order to account for the ascorbic acid contributed by the ocular tissues, the ascorbic acid was also estimated at zero time. Other incubations were carried out using vitreous and glutathione which had been pretreated with *p*-chloromercuribenzoic acid (PCMB). 3 ml were shaken with 30 mg PCMB for 10 min, centrifuged and the supernatant used as above.

RESULTS

Ascorbic Acid Content of Aphakic and Partially Aphakic Eyes

Operations were performed on fifty eyes and two months later the guinea-pigs were sacrificed. Only those eyes in which there were no apparent signs of inflammation, or abnormalities other than the operation scar, were used. It was found that some eyes were completely aphakic, whereas others contained regenerating lens tissue. The latter will be referred to as partially aphakic. Although all the animals had been maintained on a diet adequate in ascorbic acid there were wide fluctuations in the ascorbic acid blood levels and therefore the only true comparison of ascorbic acid changes are those between the operated eye and the normal eye of the same animal. The results of the analyses of the aphakic eyes are shown in Table 1 and those of partially aphakic eyes in Table 2.

TABLE 1. THE MEAN ASCORBIC ACID CONTENT OF TISSUES FROM APHAKIC EYES AND NORMAL EYES FROM THE SAME ANIMALS

Tissue	Number of eyes	Aphakic eyes. Ascorbic acid (mg/100 g)	Control eyes. Ascorbic acid (mg/100 g)	Blood. Ascorbic acid (mg/100 ml)
Aqueous	3	10·41 ± 1·83	15·30 ± 1·62	0·92 ± 0·12
Vitreous	8	11·05 ± 1·61	17·78 ± 0·77	0·75 ± 0·09
Sclera	8	14·93 ± 1·69	20·13 ± 0·87	0·75 ± 0·09
Retina	6	23·60 ± 1·46	25·70 ± 1·33	0·74 ± 0·12
Choroid	6	26·55 ± 2·79	28·40 ± 1·64	0·86 ± 0·07
Ciliary body and iris	5	20·86 ± 1·65	34·26 ± 5·18	0·81 ± 0·10
Cornea	8	25·51 ± 2·42	39·49 ± 2·51	0·75 ± 0·09

The figures given are the arithmetic means and the standard errors.

TABLE 2. THE MEAN ASCORBIC ACID CONTENT OF TISSUES FROM PARTIALLY APHAKIC EYES AND NORMAL EYES FROM THE SAME ANIMALS

Tissue	Number of eyes	Partially aphakic eyes. Ascorbic acid (mg/100 g)	Control eyes. Ascorbic acid (mg/100 g)	Blood. Ascorbic acid (mg/100 ml)
Lens	10	25·96 ± 2·76	10·34 ± 0·46	0·85 ± 0·08
Aqueous	7	17·71 ± 4·25	16·39 ± 1·69	0·85 ± 0·11
Vitreous	10	17·01 ± 2·30	17·95 ± 1·83	0·85 ± 0·08
Sclera	10	19·48 ± 2·25	19·53 ± 1·83	0·85 ± 0·08
Retina	8	28·55 ± 1·53	30·31 ± 2·61	0·87 ± 0·10
Choroid	9	37·89 ± 5·51	36·71 ± 3·09	0·85 ± 0·09
Ciliary body and iris	9	34·04 ± 3·45	41·03 ± 3·56	0·85 ± 0·09
Cornea	10	33·29 ± 3·22	45·14 ± 2·67	0·85 ± 0·08

Vitreous body. The mean level of ascorbic acid in the vitreous of aphakic eyes was 11·05±1·61 mg/100 g and in the control eyes 17·78±0·77 mg/100 g. The difference between these two means is statistically significant, $P<0.01$. In the partially aphakic eyes, however, the mean level of ascorbic acid, 17·01±2·30 mg/100 g, was almost the same as the corresponding controls, 17·95±1·83 mg/100 g. In all cases where the eyes were aphakic the vitreous was completely liquid, but this was not so in the case of partial aphakia. In two

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animals the vitreous was a normal gel, in the others the gel present was confined to a layer of varying thickness arising from the posterior periphery of the vitreous body.

Lens. The mean level of ascorbic acid found in regenerating lens tissue was 25·96±2·76 mg/100 g compared with a value for the control eyes of 10·34±0·46 mg/100 g; the difference between these means was statistically significant, $P<0.001$. The ability of regenerating lens tissue to concentrate ascorbic acid was very marked, because the value of ascorbic acid found in normal lenses was fairly constant. From a group of twenty-six normal eyes, some of which came from animals saturated with ascorbic acid, the level never exceeded 13·4 mg/100 g.

Cornea. Assessment of the effect of aphakia and of partial aphakia on the cornea is complicated by the presence of scar tissue, peripheral vascularization and the variation in ascorbic acid levels between the corneae from different animals. The mean ascorbic acid value in the aphakic corneae was 25·61±2·41 mg/100 g, which was 36·4 per cent lower than the mean level of 39·49±2·51 mg/100 g found in the controls. In the partially aphakic eyes the mean value was 33·29±3·22 mg/100 g; this was 26·3 per cent lower than that of the corresponding controls, which was 45·14±2·67 mg/100 g. In both these series some of the animals had been saturated with ascorbic acid. In control operations in which the cornea was incised but the lens not removed, the healed corneae had a mean ascorbic acid content of 26·32±5·66 mg/100 g, which was 26·0 per cent higher than the corresponding control with a level of 20·89±4·21 mg/100 g. These animals had not received ascorbic acid supplementation.

Sclera. The mean ascorbic acid level in the aphakic eye was 14·93±1·69 mg/100 g, whereas the control level was 20·13±0·87 mg/100 g. The difference between these two means is statistically significant, $P<0.02$. There was no appreciable difference between the means of the partially aphakic eyes and their controls, which had values of 19·48±2·25 and 19·53±1·83 mg/100 g respectively.

Iris and ciliary body. The mean level of ascorbic acid in the combined iris and ciliary body from the aphakic guinea-pig eyes was 20·86±1·65 mg/100 g compared with the control value of 34·26±5·18 mg/100 g. The difference between these two means is just significant, $P<0.05$. The mean levels in the partially aphakic and the control eyes were 34·04±3·45 and 41·03±3·56 mg/100 g respectively; this difference was not significant. The iris and ciliary body were analysed separately in the case of bovine and rabbit eyes. The value for the bovine iris was 24·42 mg/100 g and for the ciliary body 29·80 mg/100 g. The rabbit iris contained 32·70 mg/100 g and the ciliary body 33·56 mg ascorbic acid/100 g.

Aqueous. There was no significant difference between the mean ascorbic acid level of the partially aphakic and control eyes, these being 17·71±4·25 and 16·39±1·69 mg/100 g respectively. The mean level of 10·41±1·83 mg/100 g in the aphakic eye was less than that of the control of 15·30±1·62 mg/100 g; owing to the small number of samples no statistical significance can be attached to this difference.

Retina. There were no marked differences in the ascorbic acid levels of the retinae from any of the guinea-pig groups. The retina from the aphakic eyes contained 23·60±1·46 mg/100 g and the control retina 25·70±1·33 mg/100 g, while in the partially aphakic eyes the retina contained 28·55±1·53 mg/100 g compared with the control value of 30·31±2·61 mg/100 g. Analyses were also made on the retinae from the eyes of rabbits, rats and cows. These results are shown in Table 3.

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TABLE 3. THE ASCORBIC ACID AND HYDROXYPROLINE CONTENT OF RETINA

Species	mg/100 g Wet retina	
	Ascorbic acid	Hydroxyproline
Guinea-pig	28·2	2·8
Rabbit	19·8	2·8
Rat	29·3	1·9
Cow*	21·7	3·2

* The large blood-vessels contained 13·8 mg hydroxyproline/100 g.

Choroid. The choroid was similar to the retina in showing no appreciable change in ascorbic acid level in aphakia. In the aphakic eye the ascorbic acid level in the choroid was 26·55±2·79 mg/100 g and in the control 28·40±1·64 mg/100 g, while in the partially aphakic eye the choroid contained 37·89±5·51 mg/100 g compared with 36·71±3·09 mg/100 g in the control.

Blood. The values given in Tables 1 and 2 for ascorbic acid levels in blood are from those animals whose corresponding eye tissues have been analysed. Animals maintained under similar conditions on a normal diet had blood values ranging from 0·28 to 1·09 mg ascorbic acid/100 ml, but the individual eye-tissue levels did not vary in direct proportion to the blood levels. When the diet was supplemented with 20 mg ascorbic acid/animal/day, the whole blood levels were within the narrower range 0·89 to 1·24 mg/100 ml and the plasma between 1·24 and 1·74 mg/100 ml. Even under these conditions where the animals had been maintained for eight weeks on saturation levels there was no direct relationship between individual plasma and tissue levels.

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The Stability of Ascorbic Acid on Incubation

These results are given in Table 4. Ascorbic acid was oxidized when incubated at 37° for 1 hr at pH 6·7. This oxidation was attributed to minute traces of copper, present in the A.R. salts used for the buffer. Oxidation still occurred, even when incubations were carried

TABLE 4. THE OXIDATION OF ASCORBIC ACID ON INCUBATION AT 37° FOR 1 HR AT pH 6·7

Additions	Percentage oxidized
None, aerobic	60
None, anaerobic	39
Aqueous	7
10 per cent lens homogenate	4
Vitreous	6
Vitreous + 10^{-6}M Cu^{++}	6
Vitreous + PCMB + 10^{-6}M Cu^{++}	61
10^{-5}M GSH + 10^{-6}M Cu^{++}	3
10^{-5}M GSH + PCMB + 10^{-6}M Cu^{++}	64

PCMB and GSH have been used as abbreviations for *p*-chloromercuribenzoic acid and glutathione respectively. Ascorbic acid (250 μg) was incubated in a final volume of 3 ml, to which 1 ml of vitreous humour, aqueous, 10 per cent lens homogenate or 3×10^{-5}M GSH, had been added.

out under anaerobic conditions in Thunberg tubes in an atmosphere of nitrogen. The presence of bovine vitreous humour, aqueous, lens homogenate or 10^{-5}M glutathione greatly reduced the oxidation. This stabilizing effect was lost when these were pretreated with *p*-chloromercuribenzoic acid. The oxidation was not catalysed by *p*-chloromercuribenzoic acid.

Hydroxyproline Content of Retina

These results are given in Table 3. The determination of hydroxyproline could not be made directly on a hydrolysate of whole retina owing to the presence of substances which interfered with the final colour reaction. The attempted removal of these substances before hydrolysis, by washing with water or 20 per cent urea solution, resulted in gel formation due to the removal of ions. This was prevented by washing the homogenized retina with physiological saline. The collagen in the residue could then be gelatinized by autoclaving to yield a suitable extract for hydrolysis. The analysis of the whole bovine retina by this method showed that it contained 3·2 mg hydroxyproline/100 g, which is equivalent to 23·9 mg collagen/100 g using the conversion factor of 7·46. A partial separation of the vascular tissue showed that this contained 13·8 mg hydroxyproline/100 g, equivalent to 102·9 mg collagen/100 g. The total hydroxyproline in the rat, guinea-pig and rabbit retina was of the same order as that in the cow retina.

Distribution of Ascorbic Acid in Eye Tissue

These results are shown in Table 5. All the eye tissues had a much higher concentration than the blood. In increasing order the ratios of ascorbic acid levels of tissue to blood were, for a series of guinea-pigs maintained on a normal diet, lens (13:1), aqueous (22:1), vitreous (24:1), sclera (26:1), retina (37:1), choroid (43:1), iris and ciliary body (49:1) and cornea (58:1).

TABLE 5. THE DISTRIBUTION OF ASCORBIC ACID IN THE TISSUES OF GUINEA-PIG, RABBIT AND COW EYES

Tissue	Ascorbic acid (mg/100 g)		
	Guinea-pig	Rabbit	Cow
Lens	13·4	14·7	33·7
Aqueous	16·9	12·8	18·9
Vitreous	17·8	8·9	14·7
Sclera	19·5	11·1	5·1
Retina	28·2	19·8	21·7
Choroid	31·2	36·4	15·1*
Ciliary body	33·0	33·6	29·8
Iris		32·7	24·4
Cornea	43·7	34·4	30·3

* This value is for choroid and tapetum combined.

DISCUSSION

The evidence in the literature concerning the level of ascorbic acid in aphakic eyes has been contradictory. No attempt has previously been made to differentiate between those eyes which are completely aphakic and those which contain traces of lens tissue. The results

in Table 1 show that the level of ascorbic acid in the vitreous body of the aphakic eyes was 11·05 mg/100 g, whereas the level in the control eyes was 17·78 mg/100 g, and the difference between these two means is statistically significant. In interpreting these results, however, one has to consider whether the lowered ascorbic acid level is due to the aphakia *per se* or whether it is due to some other cause incidental to the operation for the removal of the lens, such as inflammation or damage to the ciliary body. Those eyes which were only partially aphakic were considered to contain regenerated lens tissue because the weight of this tissue obtained on dissection was sometimes as much as 40 per cent of that of the normal; the lenses were usually intact on extraction but in those cases where the capsule ruptured the size of the lens delivered differed but little from that of the normal lens. Numerous reports of lens regeneration in mammals have appeared since an early observation in 1825 by Leroy-d'Etiolles (BELLOWS, 1944). The results in Table 2 show that there was no significant difference between the ascorbic acid level of 17·0 mg/100 g in the vitreous body of the partially aphakic eye and that of 17·95 mg/100 g in the control eye. The fact that the level in the partially aphakic eyes has been almost restored to normal, indicates that the lowered level in aphakia was not caused by either surgical trauma or by inflammation.

All the eyes were dissected eight weeks after operation when there were no readily apparent signs of inflammation. Of all the eyes operated on, only eight aphakic and ten partially aphakic were considered to be otherwise quite normal apart from the corneal scar. It was found that even when animals were maintained on a diet rich in ascorbic acid there were individual variations in the ascorbic acid levels and that there was no great constancy in the plasma–ocular tissue ratios. LANGHAM (1949) has found, however, good agreement between the ascorbic acid contents of the eyes from any one animal. In order to compare, therefore, the changes caused by either the complete or partial removal of the lens, the level in the operated eye has always been compared with that in its fellow eye. This is the reason for the differences between the normal values given in Tables 1 and 2.

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The ascorbic acid level in the aqueous of aphakic eyes was also less than that in the aqueous of the control eyes, whereas there was no appreciable difference in the level in those eyes containing traces of lens tissue. At the beginning of this work it was decided to study only changes in the vitreous body and the retina, but as the work proceeded it was decided to make as complete an analysis as possible. This accounts for the small number of samples of aqueous humour analysed. BOYD (1955) has shown that the difference in level of ascorbic acid in the aqueous of control and aphakic guinea-pigs is statistically significant. In this paper he states that he selected only those animals in which there was no soft lens matter. It can be seen from Table 2 that the ability of regenerating lens tissue to concentrate ascorbic acid was very marked. The difference between the mean level of 25·96 mg/100 g in the regenerating lens tissue and that of 10·34 mg/100 g for the normal eyes was statistically significant. This normal value agrees well with the values of 10·0 mg/100 g (PODESTÀ and BAUCKE, 1938) and 8·0 mg/100 g (JOHNSON, 1936). The highest value we obtained for a normal lens, even when the animal had been saturated with ascorbic acid, was 13·4 mg/100 g. RYVKINA (1940) has also shown that regenerating tissue has the ability to concentrate ascorbic acid; the level in regenerating limbs of axolotl was found to be twice that in the normal limbs. The changes in the biochemical composition of regenerating lens tissue are of interest in view of the recent work of CHANTURISHVILI (1958), and also of STEWART and 'ESPINASSE (1959), on the regeneration of the crystalline lens in rabbits.

The physical state of the vitreous body of the aphakic eye differed from that of the partially aphakic, in that the latter always contained some gel, whereas the vitreous body in

the aphakic eye was completely liquid. CRISTIANSSON (1957) and KAHAN (1958) have reported depolymerization of the mucopolysaccharides in the vitreous body of scorbutic guinea-pigs. Cristiansson has shown that the vitreous of normal guinea-pigs takes 330 min to pass through a special glass filter, whereas the vitreous from guinea-pigs which have been kept on a scorbutic diet for twenty-one days takes 30 min to filter under the same conditions. These results show that the absence of ascorbic acid undoubtedly has an effect on the physical state of the vitreous. In scurvy there is an almost complete absence of ascorbic acid, but the vitreous body of aphakic guinea-pigs still contains 11·05 mg ascorbic acid/100 g and high dietary intakes of ascorbic acid, although raising the ascorbic acid level in the vitreous did not bring about any gel formation. It would appear, therefore, that the liquefaction of the vitreous was not a direct consequence of the lowered ascorbic acid level. In the partially aphakic eyes gel was always present in layers of varying thickness at the posterior periphery of the vitreous. It appeared as though gel formation originated in that part of the vitreous adjacent to the retina and this might be evidence in favour of the proposal by SZIRMAI and BALAZS (1958) that the cells of the cortical layer of the vitreous are possibly the sites of hyaluronic acid synthesis.

The results of the incubation experiments show that the oxidation of ascorbic acid at pH 6·7, 37°, can be prevented by the presence of vitreous humour. The protective action of the vitreous humour is removed when it is pretreated with *p*-chloromercuribenzoic acid, a compound which combines with sulphydryl groups. Similar results were obtained with 10^{-5}M glutathione. BELLOWS and ROSNER (1937) have shown that the guinea-pig lens contains 138 mg glutathione/100 g. The fact that normal concentrations of ascorbic acid were found in partially aphakic eyes would indicate that the operative procedure had not caused any failure in the concentrating mechanism of the ciliary process and one can assume that the same is true for the aphakic eye. The results of both the lowered ascorbic acid and the liquefaction of the vitreous body in aphakia could be attributed to the removal of a rich source of intra-ocular glutathione, thus allowing the oxidation of ascorbic acid to dehydroascorbic acid to take place. KINSEY (1950) has shown that the half-life of dehydroascorbic acid in phosphate buffer pH 7·3 is 22 min, the lactone ring being opened irreversibly to yield diketogulonic acid. ROBERTSON *et al.* (1941) showed that depolymerization of mucopolysaccharides is brought about during the copper catalysed oxidation of ascorbic acid. Hydrogen peroxide formed during the oxidation also plays a part in the depolymerization. All the components necessary to bring about the depolymerization of hyaluronic acid, i.e. copper, oxygen and ascorbic acid, are normal constituents of the vitreous body. TAUBER and KRAUSE (1943) have shown that bovine vitreous contains approximately 26 μg per cent of copper, i.e. 4×10^{-6}M. The normal eye must contain an inhibitor to this sequence of reactions which is probably a sulphydryl compound since the inhibitor of the oxidation is removed by treatment with *p*-chloromercuribenzoic acid. Glutathione answers all these requirements, because it is present in the vitreous, it combines with copper and it reduces hydrogen peroxide.

The retina from the aphakic eyes contained 23·60 mg ascorbic acid/100 g, which did not differ significantly from the mean level in the normal eyes of 25·70 mg/100 g. Compared with the values of 15·30 and 17·78 mg/100 g in the aqueous and vitreous respectively, the retina of the guinea-pig has a much higher content of ascorbic acid. This was also found in the case of the rabbit, cow and rat. TAHATA (1937), using the dichlorophenolindophenol method of estimation for ascorbic acid, has reported an average value of 18·4 mg/100 g in guinea-pig retina. The choroid from the aphakic and normal eyes contained 26·55 and 28·40

mg/100 g which also did not differ significantly. As the values for the choroid and retina from the aphakic and normal eyes do not differ, it would appear that in these tissues the protection of ascorbic acid against oxidation is independent of the lens. According to KODOMARI (1936) the rabbit retina contains an average of 145 mg glutathione per cent and the presence of glutathione in the retina itself might therefore explain the stability of ascorbic acid in the retina of aphakic eyes.

Similar hydroxyproline contents were found in the retinae from cows, rabbits, rats and guinea-pigs. In the case of the cow, a value of 3·2 mg/100 g was obtained which is much higher than that of 0·9 mg/100 g in the posterior portion of the vitreous (BALAZS *et al.*, 1959), or 1·2 mg/100 g reported for the whole bovine vitreous by MCEWEN and SURAN (1960). There is no supporting histological evidence that this hydroxyproline in the retina represents structural collagenous fibrils, and it is possible that it was derived from the walls of the retinal vascular system. Analysis of the larger blood-vessels from four pooled bovine retinae showed that they contained 13·8 mg hydroxyproline/100 g. This, however, did not account for all the hydroxyproline in the retina.

The results set out in this paper show that if one compares the eye, completely free from traces of lens tissue, with the other eye of the same animal then a significant decrease in the ascorbic acid level of the vitreous is observed. The ambiguity in the literature would appear to have arisen either by the inclusion in the analysis of eyes which still contain some lens tissue or by failing to use the fellow eye as a control. Whether the absence of a lens from an eye over a long period of time has any effect on the size of the orb is speculative. SHAPLAND (1934) has pointed out that non-myopic eyes which develop detachment 24·6 years after needling would have been myopic had they still contained a normal lens. The difference between the level of ascorbic acid in the sclera of the aphakic eye is significantly lower statistically than that in the control eye and this difference did not exist when the eye was only partially aphakic. This might be an indication that biochemical changes occur in the sclera in aphakia, but this result is difficult to interpret, especially as changes in the ascorbic acid level were not observed in the choroid or in the retina.

In aphakia, lowered ascorbic acid levels as such would not appear to be the direct cause of any pathological change but they are an indication of a derangement in the symbiotic metabolism between the aqueous, lens and the vitreous body, since the reduction of dehydroascorbic acid, formed by the oxidation of ascorbic acid, would make a demand on the already diminished sulphydryl content of the aphakic eye.

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SUMMARY

(1) Ascorbic acid has been determined in the eye tissues of guinea-pigs, rabbits, cows and rats.

(2) There is a statistically significant decrease in the ascorbic acid content of the vitreous body in aphakic guinea-pig eyes.

(3) The ascorbic acid content of the vitreous body from partially aphakic eyes does not differ significantly from that in the control eyes.

(4) The high ascorbic acid content of the retina is not affected by the absence of the lens.

(5) Vitreous humour protects ascorbic acid from oxidation. The protective effect of the vitreous is removed by pretreatment with *p*-chloromercuribenzoic acid.

(6) Changes of the ascorbic acid level in other ocular tissues in aphakic and partially aphakic eyes have been studied. It is concluded that the lower levels found in aphakia are

due to the greater rate of loss of ascorbic acid, rather than to the failure of the concentrating mechanism of the ciliary body.

(7) The vitreous body of aphakic but not of partially aphakic guinea-pig eyes was completely liquefied.

(8) Regenerating lens tissue has a much higher ascorbic acid content than that in the normal lens.

(9) Determinations of hydroxyproline have been made on the retinae of various species.

(10) Biochemical changes in aphakia have been discussed in relationship to pathological changes in the eye.

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EFFECT OF HYPERVENTILATION ON FOVEAL CRITICAL FLICKER FREQUENCY[1]

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Abstract—The effect of voluntary hyperventilation on the relation between foveal critical flicker frequency (n) and retinal illumination (I) was investigated with circular test fields ranging in angular diameter from 2·5′ to 2° 11′. Although the basic form of the n–log I relation was unaffected, the curves as a whole were displaced upwards along the critical frequency (n) axis to higher frequencies. The amount of the displacement increased with increasing size of field from zero, for fields below about 7′ angular subtense, to 2–3 c/s for the largest field size. The results were interpreted in terms of increased foveal interaction and were discussed in relation to recent work on spatial integration in the retina.

Résumé—L'effet de l'hyperventilation volontaire sur la relation entre la fréquence critique de flicker dans la fovéa (n) et l'illumination rétinienne (I) a été examinée pour des champs circulaires, dont le diamètre angulaire variait entre 2·5′ et 2° 11′. Bien que la forme de la relation n–log I ne fût pas affectée, les courbes entières furent déplacées dans une region de fréquences plus élevées le long de l'axe de la fréquence critique (n). Le degré de ce déplacement augmentait proportionellement à la dimension du champ en partant d'une valeur zero pour un champ angulaire de moins de 7′ et atteignant une valeur de 2–3 c/s pour les valeurs angulaires plus grandes. Les résultats sont interprétés sur la base d'une interaction fovéale augmentée, et reliés aux résultats des travaux récents sur l'intégration spatiale rétinienne.

Zusammenfassung—Der Einfluss freiwilliger Hyperventilation auf das Verhältnis zwischen fovealer kritischer Flimmerfrequenz (n) und Netzhautbeleuchtung (I) wurde mit runden Testfeldern mit Winkeldurchmessern von 2,5′ bis zu 2° 11′ untersucht. Obwohl die Grundform der n–log I Funktion unbeeinflusst blieb, waren die Kurven im ganzen parallel zur Achse der kritischen Flimmerfrequenz (n) Achse nach höheren Frequenzwerten verschoben. Die Grösse dieser Verschiebung nahm mit wachsender Testfeldgrösse von Null für Felder unter 7′ Zielwinkeldurchmesser bis zu 2–3 Hz für die grössten Felder zu. Die Ergebnisse werden als verstärkte Wechselwirkung in der Fovea gedeutet und im Zusammenhang mit kürzlichen Untersuchungen über räumliche Summation in der Netzhaut besprochen.

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ALTHOUGH respiratory effects on human visual thresholds are known to occur under conditions of low and high oxygen tensions (MCFARLAND *et al.*, 1941 and 1944; HECHT *et al.*, 1946) and when the carbonic acid content (CO_2 tension) of the blood is altered (as in respiratory alkalosis and acidosis (RUBINSTEIN *et al.*, 1935; WALD *et al.*, 1942; ALPERN *et al.*, 1952), only in the former case has quantitative analysis reached the stage where it is possible to arrive at a generalization of interest to visual physiology. To a first approximation the effects of variations in oxygen tension on several types of visual threshold may be accounted for in terms of a reversible translation of the threshold/log luminance curve as a whole along the log luminance axis without vertical shift (MCFARLAND *et al.*, 1944;

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HECHT *et al.*, 1946). Observations by RUBINSTEIN and THERMAN (1935) and ALPERN and HENDLEY (1952) on the effects of respiratory alkalosis (induced by hyperventilation)[2] on the critical flicker frequency (c.f.f.) suggest that alterations in CO_2 tension may also cause a shift of visual threshold/luminance curves without changing their basic form but that the displacement probably involves a vertical component analogous to the effect of altering the size of the test field.

Rubinstein and Therman studied the effect of both luminance and field size but their published curves (for one subject) are based on data obtained over a period of several months and accurate comparisons between the control and alkalosis data cannot be made. Moreover, their measurements were restricted to the central (linear) portion of the c.f.f./log luminance (n–log I) function and to two field sizes (1° and 4°). They are also subject to possible variations in pupil size which was not controlled. Their results nevertheless suggest that the effect of respiratory alkalosis may be fairly constant over a wide range of luminance but depend upon the size of the stimulus.

Alpern and Hendley did not vary field size nor did they make any observations at the lower end of the luminance range but their averaged data (from twelve subjects) for a 2·3° centrally fixated field suggest that the effect of hyperventilation in raising the c.f.f. is constant not only over the linear portion of the n–log I function but also at the upper end of the intensity range where the relation between n and log I ceases to be linear as n approaches a maximum value. Thus, over the range of luminance studied the control and experimental curves are parallel but the latter is shifted to a higher maximum critical frequency, a result which is analogous to increasing the stimulus size and therefore consistent with Rubinstein and Therman's findings.

However, for the reasons already given, this conclusion about the relative importance of luminance and field size is at present based upon inadequate experimental data. Further investigation of the effects of both variables over a wider range of values is obviously required before more definite conclusions can be drawn. And if Rubinstein and Therman's suggestion is correct that the influence of hyperventilation on the c.f.f. is a "function for which a certain minimal number of retinal neurones are needed" it would seem particularly important to obtain some of the measurements in small test fields so as to reduce the possibilities of interaction to a minimum.

In the experiments to be reported in this paper measurements of foveal c.f.f. have been obtained over a luminance range of about three log units for circular white test fields varying in angular diameter from about 2° to 2·5′. To avoid complications due to day-to-day variations a procedure has been used which makes it possible to obtain a complete set of control and hyperventilation data in a single experimental session.

METHOD

Apparatus

The light source consisted of a tungsten-filament lamp underrun at a constantly controlled voltage. An image of the filament was focused by a lens (L_1) upon a small aperture which was in turn imaged by a further lens (L_2) in the plane of a rotating sector disk with four 45° sectors removed to give a one to one light–dark ratio in each flicker cycle. As the beam was

[2] ALPERN and HENDLEY (1952) have shown that it is only when changes in acid–base balance are produced by changes in the concentration of CO_2 in the blood that c.f.f. is affected. Changes produced metabolically (by the administration of sodium bicarbonate) have no effect. Respiratory acidosis (produced by breathing a mixture of 7 per cent CO_2 and 93 per cent O_2) causes a decrease in c.f.f.

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of very small cross-section at its point of interception by the sector disk it was possible to obtain an almost rectangular waveform. The diverging light was then collected by a photographic lens (L_3) and focused on an artificial pupil (P), 1 mm in diameter. Attached to L_3 was a rotatable disk (D) with six circular apertures to provide six different sizes of test field as seen in Maxwellian view through P. The diameters of these apertures subtended angles of 2·5′, 5′, 9′, 19′, 38′, and 1° 16′ at the eye.

Fixation was provided for in several different ways depending upon the size of the test field and the luminance level at which observations were being made. For the larger fields illuminated at moderate to high luminances a thin glass plate bearing a black spot was attached to the rotatable disk (D) containing the aperture stops. At lower luminances this was replaced by either a single red fixation point appearing in the centre of the test field or by four red spots forming the corners of a square. In the latter arrangement, which was introduced to assist fixation of the very small fields, the test patch appeared in the centre of the square. The red fixation points were reflected into the eye from an auxiliary light source by a cover slip placed at 45° to the line of sight. Their luminances could be varied by means of a rheostat so as to be just comfortably visible.

The colour temperature of the source was approximately 2700°K, as determined by a colour temperature meter. The luminance levels of the test field were measured by a monocular matching method using a visual photometer and were varied by means of calibrated neutral-density filters. All stimulus intensities (I) in this paper are expressed in terms of trolands of retinal illumination. The sector disk was mounted on the shaft of a d.c. motor and its speed of rotation accurately controlled by a Ward–Leonard speed control unit (RAPSON, 1955). Frequency calibration, in cycles per second (c/s), was undertaken with the aid of a stroboscopic tachometer.

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The apparatus was very rigidly mounted and blackened housing and baffles used to reduce stray light to a minimum. The eyepiece containing the artificial pupil projected into a darkened room in which the subject sat while making his observations. Care was taken to ensure that he received no auditory cues from the motor which, together with the sector disk and the various components of the optical system, was housed in a separate room in which the measurements were recorded.

Although most of the data reported in this paper were obtained with the experimental arrangements exactly as described above, some of the measurements were made with a slightly different type of optical system in which the light emerging from the open sectors of the sector disk was first made parallel by an achromatic lens (L_4), placed at focal distance from the disk, before being brought to a focus at the eye by another achromatic lens (L_5). In this latter arrangement the different sizes of test field (4′, 7′, 11′, 22′, 45′, and 2° 11′) were obtained by placing diaphragms in the front focal plane of L_5. Thus the field appeared sharply defined with relaxed accommodation whereas in the former arrangement it was necessary for the subject to exercise some degree of accommodation.

Procedure

The subject viewed the test field with his right eye placed immediately behind the artificial pupil (P), an adjustable chin-rest and head-supports being used to fix the position of the eye relative to the eyepiece. Each experimental session was preceded by a stay of between 20–30 min in the dark. Determinations of the c.f.f. were then made, starting with the smallest field and lowest luminance level. Before making observations for a given field and luminance level the subject viewed the test patch for 1–1½ min to allow light-adaptation to the prevailing

intensity except when the 2·5′, 4′, and 5′ fields were presented at the lowest (i.e. near threshold) intensity.

As soon as the subject was in position and ready to make an observation he signalled to the experimenter by pressing a response key. The frequency was then decreased in steps of about 0·5 c/s from a point above the fusion frequency until the subject signalled that he could just detect flicker. This procedure was adopted after preliminary trials in which the threshold was also approached from "flicker" to "fusion". The former method proved more satisfactory owing to the greater ease with which the subject could maintain fixation and preserve the light-adapted state of the fovea.

If, for any reason (e.g. blinking, loss of fixation, blurring of the field), the subject felt unable to make an accurate judgment he informed the experimenter who then repeated the trial. To begin with, each determination was based on at least five and often ten settings but, in accordance with the experience of Hecht and others, it was found that fewer readings were desirable to avoid eyestrain and fatigue. Moreover, estimates of the c.f.f. based on two or three settings agreed very closely with those based on ten settings (cf. HECHT, SHLAER and VERRIJP, 1933).

As it is recognized that variations in n–log I curves (e.g. slope and the value of n_{max}) can occur as a result of a shift in the criterion used to judge "flicker" (HECHT and SMITH, 1936) and that the appearance of the onset of flicker varies with field size (KUGELMASS and LANDIS, 1955) considerable care was taken to ensure that the subject's task was made quite explicit in a preliminary practice session. And as the c.f.f. can change while the intermittent stimulus is being observed for durations of 1 sec or less (GRANIT and HAMMOND, 1931) the stimulus duration on which the subject based his judgment was always greater than 1 sec although the exact duration was not precisely controlled.

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Using the above procedure it was found that the c.f.f. could be determined very rapidly and reliably for experienced observers over the middle range of intensities and for the larger field sizes. But even with highly practised observers difficulties were experienced in making judgments at very high and very low luminance levels and these limited the range over which measurements were eventually obtained. At luminances lower than those recorded in our graphs it was found quite impossible to maintain central fixation for sufficiently long periods to decide when flicker first appeared. Observations on the very small fields actually used (2·5′, 4′, and 5′) were considerably impeded by fixation difficulties and fading of the test patch [Troxler's phenomenon (CLEMMESON, 1944)] so that it was sometimes necessary for the subject to ask for several presentations of the stimulus before he felt able to make a judgment with confidence.

At very high luminance levels observations became difficult owing to interference set up by flicker in the surrounding field. This effect is well known (BERGER, GRAHAM and HSIA, 1958) when a bright test patch is made to flicker in a dark surround and it increases with increasing luminance of the test field until a point is reached at which the two rates of flicker become equal. Although it is possible for an experienced observer to ignore flicker in the surround when the two rates are sufficiently dissimilar, judgment becomes extremely difficult when the test field and surround flicker at the same or closely similar rates.

For a given field size and luminance level data were first obtained under normal physiological conditions and then immediately following a period of voluntary hyperventilation during which the subject increased his rate and depth of respiration. As soon as each set of control measurements had been completed for a given combination of area (A) and intensity (I) the subject was asked to increase his normal depth of respiration and to breathe to the

beat of a metronome. The metronome settings differed somewhat for different subjects according to their normal rate of respiration but the increased rate (to about 36–40 per min) was in all cases slightly more than twice the normal value. No measurement was made of the amplitude of respiration but the subjects attempted to keep this as constant as possible. As a result of preliminary trials in which the c.f.f. was determined every few seconds during hyperventilation (an extremely difficult task) it was found that the most suitable period of hyperventilation for the purpose of the experiment was half a minute.[3] This period produced highly reproducible changes in c.f.f. which remained at a fairly constant level for a sufficient length of time after the subject had ceased overbreathing for rapid measurements to be made, yet allowed a return to normal values within 2 or 3 min (see Fig. 1). Using the above procedure it was possible to obtain a complete set of control and hyperventilation data in a single session.

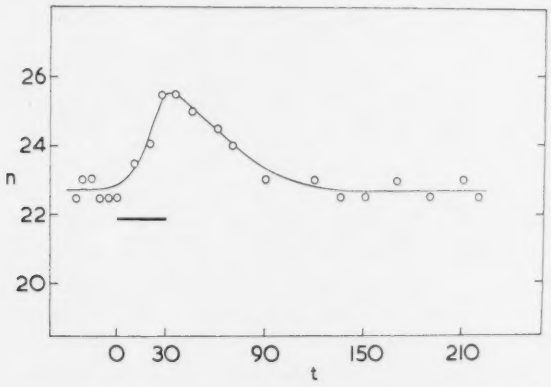

FIG. 1. Typical time course of the effect of hyperventilation on foveal critical flicker frequency (n), in c/s. The horizontal line below the curve marks the period of overbreathing (time (t) in sec).

Subjects

Most of the observations were made by the two authors, both of whom have served as observers in numerous flicker experiments undertaken over a period of several years, but data were also obtained from five other subjects for a more limited range of stimulus conditions. None of the subjects taking part in the experiment suffered from any visual disorder or other pathological condition known to affect the c.f.f. Any refractive errors were fully corrected.

RESULTS

The control data for the n–log I relation are shown as open circles in Figs. 2 and 3 for the two authors, subjects G and I, respectively. Each point is based on the average measurements for two different sessions. The curves drawn through the points display the typical features of n–log I curves for centrally fixated fields falling within the fovea. Over the range of luminance examined (about three log units) the relation between the critical frequency (n)

[3] Although the period of hyperventilation was brief the increased rate and amplitude of respiration nevertheless gave rise to some of the typical subjective symptoms of respiratory alkalosis which ALPERN *et al.* (1955) observed after about one minute's hyperventilation. This degree of hyperventilation may be expected to cause an increase in the blood pH of about 0·1–0·2 unit (DODT, 1951; ALPERN *et al.*, 1955).

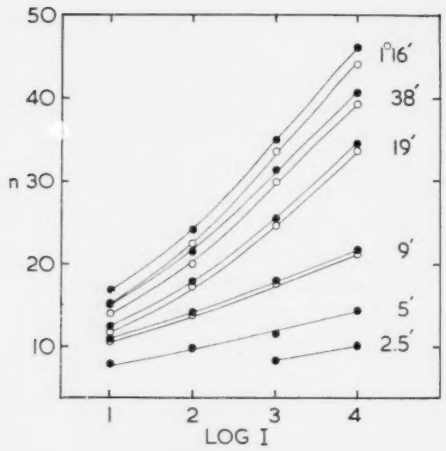

FIG. 2. Critical flicker frequency (n), in c/s, as a function of log intensity (I), in trolands, for test fields ranging in angular diameter from 2·5′ to 1° 16′. Each point represents the mean of observations from two sessions for subject G. (○): control data; (●): hyperventilation data.

and log I is approximately linear in accordance with the Ferry–Porter equation ($n=a$ log $I+b$). The general shape of the data is very similar for the two subjects and the slopes for the 1° 16′ test field are of the same order as those found by earlier workers who have used fields of similar size (HECHT and VERRIJP, 1933). Further evidence of the reproducibility of the main features of the n–log I curves in different subjects is presented in Fig. 4 (open circles), which shows the averaged data of five additional subjects for fields of 45′ and 2° 11′ angular diameter. These mean curves provide a satisfactory description of the individual curves all of which were of the same basic shape.

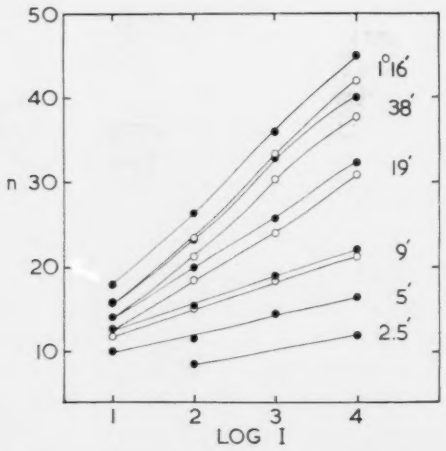

FIG. 3. Critical flicker frequency (n), in c/s as a function of log intensity (I), in trolands, for test fields ranging in angular diameter from 2·5′ to 1° 16′. Each point represents the mean of observations from two sessions for subject I. (○): control data; (●): hyperventilation data.

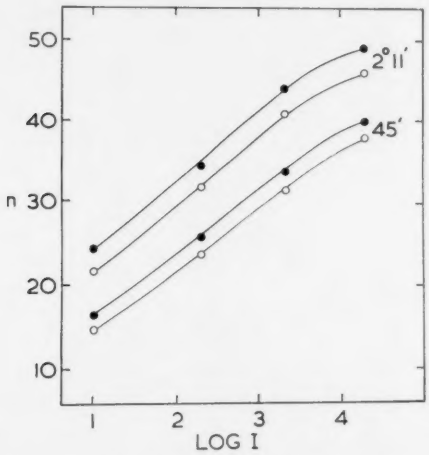

FIG. 4. Critical flicker frequency (n), in c/s, as a function of log intensity (I), in trolands, for test fields of 45′ and 2° 11′ angular diameter. Each point represents the mean of observations for five different subjects. (○): control data; (●): hyperventilation data.

Data for the smaller fields (in Figs. 2–4) are displaced downwards on the frequency axis, confirming many earlier observations that for a given value of I a decrease in A is accompanied by a decrease in n (KUGELMASS and LANDIS, 1955), but it will be noted that the n–log I curves for the very small fields have a shallower slope than those for the larger fields.

The degree of reproducibility that we were able to obtain on different occasions in the same subject is illustrated in Fig. 5 by some typical measurements for subject G. The data denoted by the filled-in circles and partly filled-in circles were obtained on two consecutive days while those denoted by the open circles were obtained a week earlier. Results for the other subject (I) were essentially the same and confirmed an earlier conclusion of HECHT

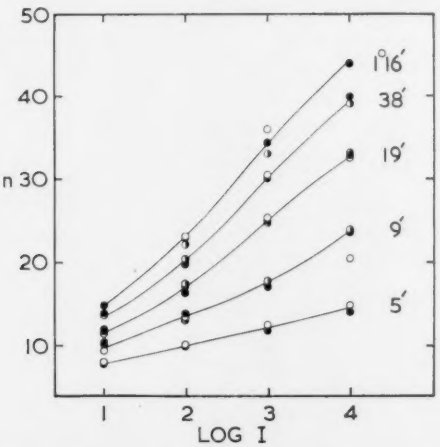

FIG. 5. Critical flicker frequency (n), in c/s, as a function of log intensity (I), in trolands, for test fields ranging in angular diameter from 5′ to 1° 16′. Reproducibility of data for subject G on three different occasions. (○): data for 1st occasion; (●): data for 2nd occasion; (◑): data for 3rd occasion.

and VERRIJP (1933) that the process of averaging n–log I data obtained on different occasions in the same subject "merely served to smooth the data without in the least distorting the relationship which they describe" (HECHT and VERRIJP, 1933, p. 255).

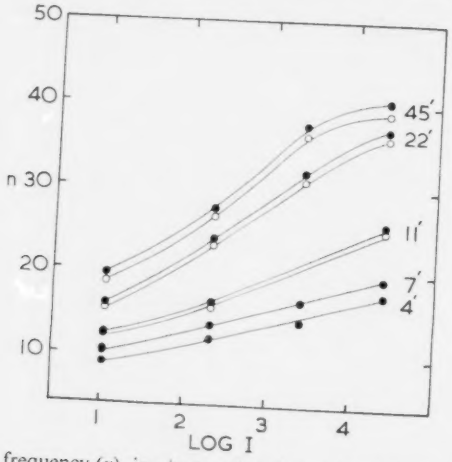

FIG. 6. Critical flicker frequency (n), in c/s, as a function of log intensity (I), in trolands, for test fields ranging in angular diameter from 4′ to 45′. Each point represents the mean of observations made in a single session by subject G two years before the data of Fig. 2 were obtained for the same subject. (○): control data; (●): hyperventilation data.

Some indication of the reproducibility that was observed over longer periods of time can be obtained by comparing the control data of Fig. 2 and 5 with Fig. 6, which shows similar data for subject G collected 2 years earlier. The field sizes were not the same as for the later measurements and a different optical system was used (as previously described) but the data conform closely to the same general pattern. Additional data also obtained 2 years ago for the same subject are shown in Fig. 7 for a wider range of intensities and a larger

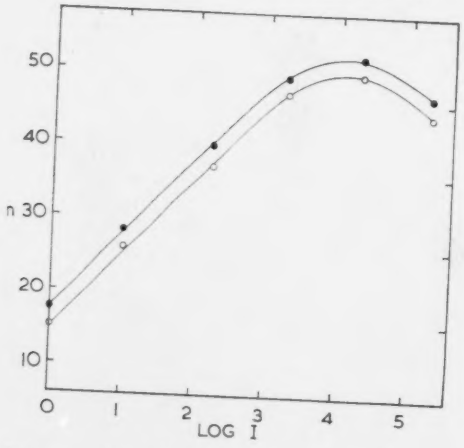

FIG. 7. Critical flicker frequency (n), in c/s, as a function of log intensity (I), in trolands, for a test field of 2° 11′ angular diameter. Each point represents the mean of observations made by subject G in a single session two years before the data of Fig. 2 were obtained for the same subject. (○): control data; (●): hyperventilation data.

field. These not only confirm the reproducibility of the measurements but show the departure from linearity at very high luminances. As the intensity is increased a maximum c.f.f. is reached beyond which further increase in intensity results in a decline (cf. HECHT and VERRIJP, 1933).

Turning next to the data obtained under hyperventilation (denoted by filled-in circles, except in the case of the control data of Fig. 5), it is seen that the basic form of the n–log I relation is unaffected by hyperventilation but the data for fields greater than about 5′ angular subtense are displaced upward along the frequency axis to higher critical frequencies. This effect appears to be highly reproducible on different occasions in the same subject (Figs. 2, 5, 6 and 7) and in different subjects (Figs. 2, 3 and 4). For a given area the effect is approximately constant over a luminance range of about three log units and, judging from the results obtained with the 2° 11′ field (Fig. 7), it appears to hold over a considerably wider range (five log units).

Although the increase in c.f.f. for a given area is constant with varying I it is clear that it depends upon the size of field and that for fields of about 7′ or less angular subtense $\Delta n=0$. To illustrate this dependence the data for subjects G and I have also been plotted in the form of n–log A curves in Figs. 8 and 9. As first pointed out by GRANIT and HARPER

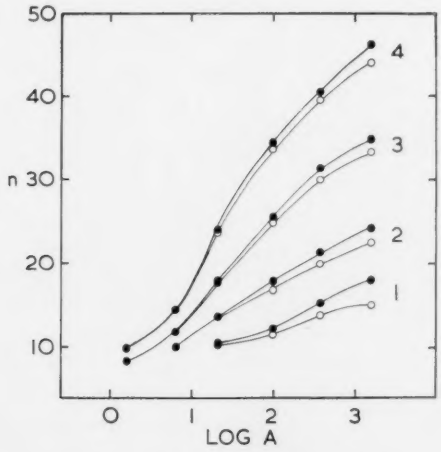

FIG. 8. Critical flicker frequency (n), in c/s, as a function of log stimulus area (A) for four intensity levels. Log $A=0{\cdot}2$ corresponds to an area of angular diameter equal to 2·5′. Average data for subject G. (○): control data; (●): hyperventilation data.

(1930), the relation between n and log A is very approximately linear for a given intensity over part of the range examined in accordance with their equation, $n=c \log A+d$, although the complete curve is probably sigmoid in shape and the slope of the linear segment of the curve decreases with decreasing I. Expressed in terms of the n–log A relation the effect of hyperventilation is to cause an increase in slope at all the luminance levels studied.

DISCUSSION

It is quite clear from the above results for the larger sizes of field that the effect of hyperventilation cannot be described in terms of a shift of the n–log I curve along the log I

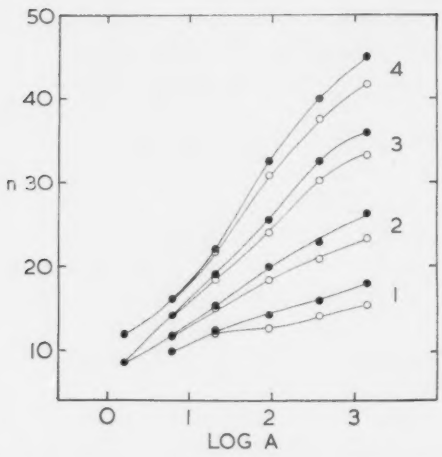

FIG. 9. Critical flicker frequency (n), in c/s, as a function of log stimulus area (A) for four intensity levels. Log $A = 0{\cdot}2$ corresponds to an area of angular diameter equal to 2·5′. Average data for subject I. (○): control data; (●): hyperventilation data.

axis. In contrast to the effects of altered oxygen tensions on various threshold luminance curves for the fovea, the parallelism of the control and experimental curves (for comparable field sizes, i.e. about 1°) is maintained at all luminance levels studied, over both the linear and non-linear portions of the n–log I relation. Under hyperventilation the slope of the linear portion of the curve is essentially the same as under normal conditions and it is interesting to note that the actual value of the slope (about 10 in all subjects) for the 1° 16′ and 2° 11′ fields is very similar to the slope of the averaged data obtained by Alpern and Hendley (10 for a 2·3° field) and Rubinstein and Therman (about 11 for a 1° field). Thus over the luminance range in which the Ferry–Porter law holds the slope constant (a) is unaffected by hyperventilation although the position of the curve on the ordinate is changed. The magnitude of the shift is subject to some individual variation due, presumably, to variations in the rate and depth of respiration as well as to differences in the functioning of the visual system.

The upward shift of the n–log I curves for field sizes of 19′ and above is essentially similar to the kind of displacement which occurs when the area of centrally fixated fields is increased, for as HECHT and CROZIER *et al.* (1936, 1936–1937) pointed out, increasing the area of the stimulus does not affect the basic shape of the n–log I curve so far as cone flicker is concerned. In Hecht's words: "the tendency for an increase in maximal frequency with area is the expression merely of the value of a constant which determines the position of the data on the frequency axis." However, although this conclusion appears to be approximately true of centrally fixated fields of about 20′ or more angular diameter (HECHT *et al.*, 1936; KUGELMASS *et al.*, 1955; ROEHRIG, 1959) it is certainly not true of very small foveal fields under the conditions of the present experiment for the slopes of the n–log I curve, for 9′, 7′, 5′, 4′, and 2·5′ fields are certainly much shallower than those for larger fields. PIÉRON (1935) and one or two other investigators have also observed changes in slope with decreases in the size of foveal fields.

The most significant feature of the n–log I and n–log A data as a whole is the gradual increase in the effect of hyperventilation with increasing size of field, from zero for fields of

a few minutes' angular subtense to 2–3 c/s for fields of 1°–2°. The only other investigator who has studied the effects of hyperventilation on small foveal fields is JORGENSEN (1955), but it is not possible to make any precise comparisons with his results (obtained at a single luminance level) owing to differences in experimental conditions and lack of information concerning his c.f.f. However, it would appear that the general trend of his data (plotted in the form of percentage increases) for fields ranging from about 2′ to 1° angular diameter is similar to the present results. But whereas Jorgensen found that the hyperventilation effect declined as the field size was further increased we find no evidence of this; the effect is still continuing to increase with the 2° 11′ field. Our data for fields larger than 1° are thus in agreement with those of RUBINSTEIN and THERMAN (1935), who used a 4° field, and ALPERN and HENDLEY (1952), who used a 2·3° field.

In accordance with the general idea that c.f.f. is a function of the total number of activated neural "elements" (CROZIER *et al.*, 1936–1937), the upward shift of the n–log I curves may be interpreted as due to a temporary increase in the number available. And as the human ERG is known to be affected by hyperventilation (ALPERN, 1955; DODT, 1951) and the discharges down the optic nerve fibres from the retinal ganglion cells appear to lose their "flickering" quality at a frequency close to the ERG and sensory fusion frequencies (ENROTH, 1952 and 1953; DODT, 1951; DODT and ENROTH, 1953; DODT and WADENSTEN, 1954; HECK, 1957), it seems reasonable to suppose that hyperventilation may increase the availability of elements in the retina itself. (The alternative, if the correlations between the sensory and electrophysiological data are accepted,[4] would be to assume that the higher visual centres are able to split up a discharge already "fused" in the nerve (RUBINSTEIN and THERMAN, 1935). That interaction of retinal neurones may be facilitated by respiratory alkalosis is suggested by analogous effects observed elsewhere in the central nervous system (LEHMANN, 1937; DUSSER DE BARENNE *et al.*, 1937; LORENTE DE NO, 1947) but it is not possible at present to be more specific about the type of interaction involved.

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One possible starting point for further analysis of the area effect by sensory methods is suggested by recent work on retinal integration, particularly by WEALE's (1957) proposed generalization of the Ferry–Porter law to take into account the total effective quantity of light rather than stimulus intensity alone. When the exposure time is constant the effective quantity of light (Q) is given by the familiar expression for the area/intensity relation, viz. IA^p, where I and A have their previous meanings and p is the index of spatial integration for the particular retinal region under test.[5] As the critical frequency (n) has been determined in the present investigation for various field sizes and luminance levels it is possible, for a fixed value of n, to derive values of log I corresponding to each area and thus consider the effect of hyperventilation in terms of the resulting area/intensity relation. Some illustrative data are shown in Fig. 10 for a constant value of $n=10$ c/s. They were not derived from the n–log I measurements previously discussed but from a separate experiment, for it is not possible to obtain log I and log A values from Figs. 2 and 3 over a sufficiently wide range to

[4] Although electrophysiological data from the ERG and retinal ganglion cells suggest that the basic form of the n–log I and n–log A functions is largely determined by the retina, correlations with the sensory data are far from perfect and other evidence (SHERRINGTON, 1904) suggests that under certain conditions the central visual pathways may limit flicker recognition. However, it is difficult on the basis of existing knowledge of the cerebral effects of respiratory alkalosis and of the physiology of the central visual pathways to see how the area effect can be satisfactorily accounted for in terms of central processes. It is also difficult to account for the area effect in terms of a shift in the criterion used to judge flicker.

[5] In a more recent paper, WEALE *et al.* (1959) no longer consider stimulus area as such but instead the total number of cones covered (and presumably stimulated) by the test field.

define the function. The apparatus for this additional experiment employed a neon-tube as a test source and was of essentially similar design to that described in detail elsewhere by GRANGER and IKEDA (1960). The control data of Fig. 10, denoted by open circles, show that, with an increase in log A, log I decreases fairly rapidly at first and then more slowly as the size of the test field extends beyond the rod-free area of the retina. Here it is worth noting that the similar plots of ROEHRIG (1959) for much larger centrally fixated fields reveal a more or less linear relation between log I and log A with an extremely shallow slope for the lowest critical frequency (25 c/s) examined.

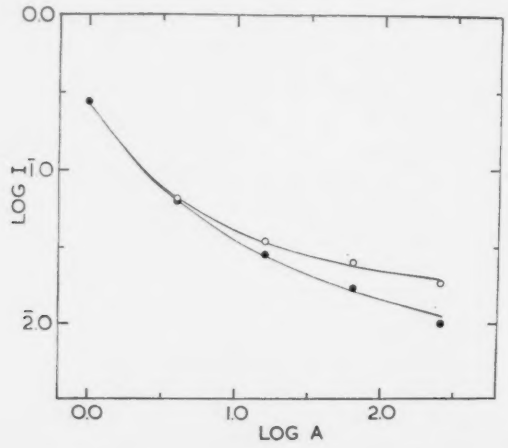

FIG. 10. Log intensity (I) as a function of log area (A), for a fixed critical flicker frequency (n) of 10 c/s. Log $I=0$ corresponds to a retinal illumination of 100 trolands. Log $A=0$ corresponds to a stimulus area of angular diameter equal to 5′. (○): control data; (●): hyperventilation data.

The significant feature of the data in Fig. 10 is that the gradient $d(\log I)/d(\log A)$ increases following hyperventilation. It is tempting to conclude from this plot, on analogy with the well-known area/intensity functions for the absolute and increment thresholds, that the effect of hyperventilation is temporarily to increase spatial integration over the range where this is incomplete, i.e. where the gradient of the log I/log A curve is less than 1. However, the relation between area and intensity in our own and other flicker data is much more complicated than Fig. 10 might suggest so that one cannot generalize very far at present. For instance, the shape changes to some extent at different critical frequency levels and the exact relation between log I and log A is difficult to determine for low A values.[6] Other reasons which make it rather pointless to pursue this type of analysis further with the existing data is that the amount of hyperventilation could not be accurately controlled and varied over a wide range and relevant biochemical data (e.g. blood pH, pCO_2) were not available to relate quantitatively to the visual changes. It may nevertheless serve as a useful basis for further experimentation.

It would be highly interesting to determine if the threshold changes observed by WALD *et al.* (1942) and ALPERN and HENDLEY (1952) under hyperventilation are due to increased spatial summation and whether the effects would vary with the eccentricity of the test field,

[6] I.E. the slopes of the n–log I curves for very small fields cannot be accurately determined with the present experimental arrangement.

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in accordance with the known differences in the integrating power of the foveal and extra-foveal regions of the retina. Similar experiments could be undertaken with the increment threshold and the effects of hyperventilation studied for different stimulus-durations, adapting-intensities, and other conditions known to affect spatial summation.

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THE VEILING FUNCTION AND NON-ADDITIVITY IN FLICKER-FUSION[1]

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(*Received 25 September 1960*)

Abstract—The following finding is reported: Given a flicker-fusion brightness match between any monochromatic color and white, the physical brightness of a second monochromatic light, which is added to the first one, is veiled or suppressed by it. That is, the second light fails to cause the immediate reappearance of flicker which would be predicted on the basis of the theory of strict additivity of brightnesses. The resultant curve is called the veiling function. It is reported for two observers, under various conditions.

Résumé—On expose le résultat suivant: dans une égalisation de luminosité obtenue par fusion du papillotement entre une couleur monochromatique et du blanc, la luminance physique d'une seconde lumière monochromatique que l'on ajoute à la première est voilée ou supprimée par elle. Cela signifie que la seconde lumière ne produit pas la réapparition immédiate du papillotement que l'on prédirait sur la base de la théorie d'addition stricte des luminances. La courbe ainsi obtenue est appelée "fonction de voile"; on donne les résultats pour deux observateurs, dans des conditions variées.

Zusammenfassung—Besteht bei der Fusion monochromatischen und weissen Flimmerlichtes Helligkeitsgleichheit, so wird die Helligkeit eines zusätzlichen monochromatischen Lichtes, das ersterem hinzugefügt wird, verschleiert oder unterdrückt. Das heisst, dass das zusätzliche Licht die Verschmelzungsfrequenz nicht heraufsetzt, wie es auf Grund der Theorie der strengen Additivität der Helligkeit zu erwarten wäre. Die sich ergebende Kurve wird Verschleierungsfunktion genannt. Es wird über eine Untersuchung mit zwei Beobachtern bei verschiedenen Bedingungen berichtet.

INTRODUCTION

THIS is a preliminary report. It describes what appears to me to be a somewhat different[3] and potentially fruitful experimental approach to the study of flicker-fusion phenomena. Because of its simplicity, the results can very readily be checked. The data to be reported are as yet incomplete; it is primarily the method and the ideas which it suggests that I believe to be important.

In the midst of a larger study on flicker perception in anomalous color vision, it seemed worth while to re-examine the concept that the disappearance of visual flicker between any two alternating lights, upon the adjustment of the brightness of one, reflects the fact that the two lights are then of equal brightness.

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[1] This work was supported by a special traineeship #BT–436 from the National Institute of Neurological Diseases and Blindness, Public Health Service.

[2] Present address: Department of Ophthalmology, University of Miami School of Medicine, Miami, Florida.

[3] Search of the literature has revealed few anticipatory experiments: but see LANDIS, 1953; and esp. PIÉRON (1939a, 1939b) and GALIFRET and PIÉRON (1950).

This concept has been examined many times before (IVES, 1912), though it is still not yet entirely understood. The usual procedure is to compare critical-flicker luminosity curves to those obtained by other methods such as the methods of threshold visibility and/or of heterochromatic brightness matching. Sometimes, though less often, critical-flicker data are checked for their internal consistency; that is, two lights equated by fusion with a third light are compared by flicker with each other.

The flicker methods generally take the following form. Some (any at all) reference white light (W) is presented at a fixed brightness level, B(W), in temporal alternation with a reasonably monochromatic light, (λ_1), of variable brightness, B(λ_1). The two lights are presented in exactly superimposed visual fields. The rate of alternation between them is fairly slow, well below the flicker-fusion rate (persistence of vision) of each light presented separately. Thus, at first, flicker is clearly visible between them: first white, then color, then white, then color, and so on. This flicker is due primarily to brightness differences and secondarily to color differences. In raising the brightness of λ_1, a normal, well-trained observer will generally see the flicker due to color differences disappear first. That is, the field will take on a uniform color somewhere between that of W and that of λ_1.[4] Next, as the brightness of λ_1 is increased still more, all the flicker will disappear. That is, the visual field will finally come to appear completely homogeneous and at rest. This is the point of critical-flicker-fusion. The brightness of λ_1 is now said to be "equal" to that of W, i.e.

$$B(\lambda_1) = B(W).$$

The relative foveal flicker luminosities of λ_1, taken through the visible spectrum, constitute the well-known photometric luminosity curve, the V_λ curve of widespread scientific and industrial significance. Though other methods have been used to obtain approximations to this curve, the critical-flicker methods are most commonly used because of their greater reliability (IVES, 1912).

Now, let us look for a moment at the meaning of the statement that at fusion the brightnesses of the two lights are equal. It is the nature of this equality which we wish to highlight here.

Equality, in the mathematical sense, cannot justly be extended to psychological and psychophysical domains without circumspection. For example, in the heterochromatic matching studies, the "equality" of brightness seems to be given directly and solely by the fact that the observer reports them to be equal; this equality is, above all, a phenomenal one. Nevertheless, it is not quite sufficient in itself. Even here, we must make an additional assumption; namely that the psychophysical events which lead up to this experience of equality are themselves stable, or are themselves also equal in an operationally different sense of equality. Similarly, in the visual threshold measurements where the subject either senses light or he does not, we are permitted to infer "equality" only because of our belief in the stability of those events which determine the psychophysical limen. Likewise, once again, in the flicker experiments, where the subject experiences fusion, our inference of "equality" has the complex assumption at its base of the stability (equality) of the determining psychophysiological events.

After some experience with those various methods, we are justified in making a further inference: those processes which we must assume to be stable in the case of the matching experiment are perhaps more heavily laden with purely psychological components than are

[4] Such a judgment is definitely also possible for color-deficient observers, though it is generally uncertain.

the corresponding presumably stable processes behind the flicker experiments. These latter, we find, have much greater reliability than the former components, and thus seem to possess a correspondingly greater objectivity. It is this seeming objectivity which tempts us further to apply a rigor of mathematical analysis to the flicker "equality" which we might not so readily apply to the phenomenal "equality".[5]

Thus, using the term equality in the strict mathematical sense, we may deduce, *inter alia*, the following corollary to the basic assertion of flicker fusion.

Corollary: *that any further light added to or subtracted from either of the two fused lights will re-establish the flicker.*

That is, it will (or should) destroy the fusion. This corollary is usually thought to be quite conclusively shown by the fact that the brightness control on λ_1 must be extremely delicate. The standard deviations of the brightness adjustments of λ_1 are indeed the smallest of any comparable visual psychophysical judgment yet known. This holds equally well for whichever of the two lights is variable.

However, and this is critical, there is nothing in the above discussion that restricts us in our choice of lights. Suppose, for example, that after fusion has been obtained, we add some variable amount of $\lambda_2 \neq \lambda_1$ to λ_1, that is we add light of some other wavelength, as if we were to seek to maintain fusion between B(W) and $[B(\lambda_1)+B(\lambda_2)]$. Suppose we hold B(W) and $B(\lambda_1)$ fixed at the level appropriate for fusion, then it follows exactly from the above corollary, that any amount of $B(\lambda_2)$ added *regardless of wavelength*, certainly, in a psychophysical sense, any amount which exceeds, say, thrice the variability (standard deviation) of $B(\lambda_1)$, would necessarily destroy fusion. This is true precisely because the basic expression is entirely independent of wavelength.

Should flicker fail to recur under these circumstances, whatever other relevance this may have,[6] it would cause us at the very least to reject the above corollary, and to replace it with another which is restricted to specific lights or wavelengths. That is, the term "equality" in the flicker-fusion experiment would lose some of its vigor. Moreover, this finding would also cast doubt on all the other mathematical corollaries of this equality, in particular, on the properties of association and of additivity.

THE PRESENT EXPERIMENT

This experiment, then, was conducted. The flicker-fusion of $B(W)=[B(\lambda_1)+B(\lambda_2)]$ was investigated, for $B(\lambda_2)>3\,\sigma B(\lambda_1)$, where $\sigma(B\lambda_1)$ is the standard deviation of the $B(\lambda_1)$ setting. The Wright colorimeter was used (WRIGHT, 1948).[7] The reference white was standard illuminant A at 2854°K, yielding at the pupil (diameter about 3 mm) approximately 358 cd/m^2. λ_1 was obtained from the beam of the "green" primary. λ_2 was obtained from either the "blue" or the "red" primary beams as the case may be. Due to structural considerations, only a restricted region of the visual spectrum, λ_2, could be sampled for any given λ_1. Hence

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[5] We call that brightness defined by the phenomena of flicker-fusion equality "photometric brightness", to distinguish it from brightness defined in other ways, say by matching studies or threshold visibility. We hope, certainly, that the various operational definitions eventually give rise to reasonably equivalent values, but we must admit that this does not go without saying.

[6] I would suggest, for example, that it might be related to the opposition of colors, as in the Hering theory.

[7] It is necessary, in this experiment, that λ_1 and λ_2 both flicker at exactly the same rate, a condition met perfectly by this instrument. My very special gratitude is due to Professor Wright for allowing me to use his instrument in this work.

there are large gaps in the individual curves.[8] However, considered *in toto*, the curves do overlap sufficiently well so as to give some idea of the general tendency of the data. Flicker was obtained by using a 1/2 on–off white rotating disk, which alternately reflected W into the eyepiece (simultaneously obscuring λ_1 and λ_2) or passed $\lambda_1+\lambda_2$ into the eyepiece (simultaneously obscuring W, i.e. failing to reflect W into the eyepiece). The brightnesses of λ_1 and λ_2 were controlled by wedges. λ_1 was first matched very carefully to W by observing the disappearance of flicker. Then λ_2 was added gradually until flicker just became visible once again. The data are treated in the usual manner, and appear in the accompanying figures.[9]

Two observers were employed; the author was the principal investigator (obs. D); but being severely deuteranomalous, it was necessary to use a normal control subject (obs. N) for at least some of the curves if only to demonstrate that the effect was not a peculiarity of anomalous color vision.

RESULTS

The results clearly indicate that substantial amounts of $B(\lambda_2)$ can be added to the fused brightness match *before flicker returns.*[10] Thus, two "equations" seem to hold simultaneously.

$$B(W) = B(\lambda_1) \tag{1}$$

$$B(W) = B(\lambda_1) + B(\lambda_2). \tag{2}$$

Moreover, it is positively shown that this contradiction is not peculiar to anomalous color vision, but occurs in normal observers as well.

The actual amounts of $B(\lambda_2)$ for selected λ_1's are shown in the figures; where λ_1 is given in the upper right-hand corner; λ_2 is given as the abscissa; and the reciprocal of the logarithm of the relative energy of λ_2 which could be introduced just up to the recurrence of flicker, is given as the ordinate. The ordinate units are arbitrary, the maximum of each graph was set approximately at zero for convenience. Each point is an average of a minimum of three determinations. Fig. 1(a) to Fig. 1(f) show the results for obs. D for selected wavelengths of λ_1.[11] Fig. 1(b) to Fig. 1(f) were taken at the same brightness level, and are thus directly comparable. Fig. 2(a) and Fig. 2(b) show two comparable curves for obs. D and obs. N. And Fig. 3 shows comparable curves for obs. D at two different brightness levels.

In interpreting these curves, it is first of all important to realize that the variability of the $B(\lambda_2)$ setting is only slightly greater than that of the $B(\lambda_1)$ setting; in fact, for obs. N, the two were often exactly the same.

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[8] It is because of this limitation in the data that I consider the present report to be preliminary. There is nothing in principle against obtaining more complete curves; it is only that the colorimeter could not be readily adapted for this purpose.

[9] The author wishes to thank Dr. Frank J. J. Clarke, Technical Optics Section, Imperial College, for the requisite instrument calibrations.

[10] For example, the settings for obs. D at $\lambda_1=500$ mμ+$\lambda_2=690$ mμ, $\lambda_1=565$ mμ+$\lambda_2=470$ mμ, $\lambda_1=663$ mμ+$\lambda_2=480$ mμ and $\lambda_1=690$ mμ+$\lambda_2=470$ mμ were such that λ_2 was at the maximum brightness which could be supplied by the colorimeter (wedge setting 21 cm). Moreover, the dearth of observations in the blue is because of the insufficient energy in this part of the spectrum in comparison with the relatively high brightness of the $B(\lambda_1)=B(W)$ match. The curve at 460 mμ was taken at a reduced brightness level for this reason.

[11] These particular wavelengths were chosen for reasons outside the present context; however, they do seem to sample the spectrum reasonably well, which is all that is necessary.

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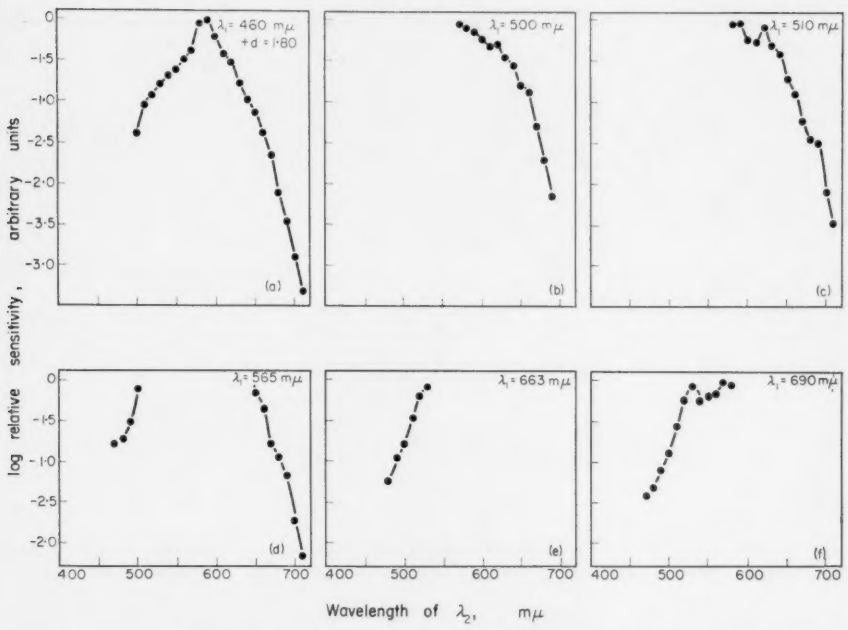

FIG. 1. The veiling function of a severely anomalous trichromate for six different wavelengths of λ_1: (a) 460 mμ; (b) 500 mμ; (c) 510 mμ; (d) 565 mμ; (e) 663 mμ; (f) 690 mμ.

DISCUSSION

I call these curves "veiling" functions or "veiling" curves simply to describe, in as unbiased a way as possible, the fact that the presence of a given amount of λ_1 in the flicker-fusion context seems to screen out, to hide or to "veil" the presence of certain amounts of λ_2 when simultaneously introduced into exactly superimposed and synchronized visual fields. Light is somehow present, one might say, without luminosity. It should be stressed that the possibly related term inhibition cannot justly be used here, because this latter term clearly implies a specific physiological event, whereas I wish only to describe a psychophysical occurrence, leaving all causal discussions for another time.

Before discussing the graphs, the question may arise as to whether the relative amounts of λ_2 which have been veiled are above the "threshold" for the particular level of adaptation maintained by the brightness of the fused field. But this is a spurious question because the corollary holds (in the mathematical sense) that *any* amount of light added should destroy fusion, not any amount above some momentary threshold. Recall, for example, that *any* amount of λ_1 added (over and above the variance) does in fact destroy fusion; what, then, should be different about λ_2? To invoke the concept of adaptation level for λ_2 but not for λ_1 would be an *ad hoc* procedure at best. In any case, there is nothing in the presently accepted statement of flicker-fusion equality which expresses anything about adaptation level, just as there is nothing about the color of the light used.

In this same connection, some of the qualitative findings may be of interest. It was possible, for example, to switch directly from B(W) to B(λ_2) alone (with no inherent time-lag) and to ask the subject to report what was seen. In all cases, the veiled light was seen readily and in full color, indicating that it was well above cone threshold.

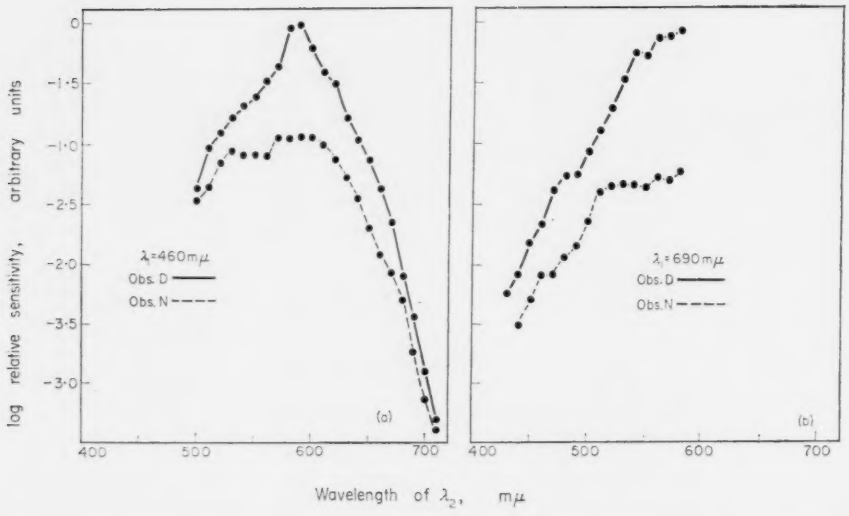

FIG. 2. The veiling function of a normal observer for two different wavelengths of λ_1 compared with the similar curves of a severely anomalous trichromate: (a) 460 mμ; (b) 690 mμ.

In addition, the effect of retinal position was marked; the fovea was quite obviously more sensitive to the restoration of flicker than the periphery. This might suggest that it is the color flicker which returns rather than the brightness flicker. But, first of all, this distinction, in the recurrence of the flicker, could not readily be made on the phenomenal level. Secondly, in view of the growing distinction (particularly in the blue) between luminosity and hue, it is of importance to note that when adding blue as λ_2 (say below 490 mμ) the color of the visual field turned markedly bluish, even completely magenta for λ_1 above 650 mμ, long before any flicker reappeared. This was true for both observers. This addition of hue before luminosity was also apparent for the normal observer with the red as λ_2 (say above 640 mμ), though it was much less obvious. For obs. D, all wavelengths, other than the blue, seemed to shift the color vaguely towards the yellow, the yellow–green, or the yellow–red, but without any reliable distinctions. It was clear, nevertheless, that one could determine two consecutive thresholds for both observers, the first being for the addition of hue and the second being for the restoration of flicker. This argues, thus, very strongly against the idea that it is the color flicker rather than the brightness flicker which returns.

Finally, it was felt that the rectangular 1° 20′ field was very large, because flickering at the edges was often a disturbing factor. This experiment should probably be done with a very much smaller visual field in the future. A few observations taken with an approx. 30′ field were found to be very satisfactory. The effects of steady fixation were also quite pronounced, and it was found best to use a relaxed rather than a rigidly fixed regard. It is probable that the suggestion of MAHNEKE (1957)[12] to use discontinuous rather than continuous viewing in flicker measurements will be of use here.

[12] Mahneke's additional point, that the appearance of flicker is a more reliable index than its disappearance, directly supports the experimental method used here.

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Turning now to the figures, the conclusion seems unavoidable that the corollary at issue has been proven false, in the sense of the crucial experiment.[13]

The basic questions which remain are the confirmation of the exact shape(s) of the veiling function and the determination of its psychophysiological nexus. Since the present data are incomplete, however, satisfactory answers to both these questions must be put aside for the moment.

Nevertheless, a few things do emerge. In general, we were unable to take the λ_2 wavelengths near enough to λ_1 to tell us exactly what occurs in this vicinity; but there is nothing elsewhere in the curves to suggest that the obvious hypothesis—that $B(\lambda_2) \rightarrow \sigma(B\lambda_1)$ as $\lambda_2 \rightarrow \lambda_1$—would not prove to hold true, should we eventually be able to make the test. However, the many obvious flex points [a few of which have the very convincing reliability of $\pm 0{\cdot}005$ in log kI, e.g. Fig. 1(b) at 620 mμ] attest to the fact that at least some additional factors are operative other than the frank dissimilarity of λ_1 and λ_2. Actually, the magnitudes of the humps in Fig. 1(c) at 610 mμ and Fig. 1(f) at 540 mμ may be exaggerated, because of the poorer reliability at these wavelengths. This, in turn, is almost certainly related to the insertion of auxiliary density filters here in order to extend the range of the wedge. The consequent sudden shifting of the wedge readings from one end of the wedge to the other—with the resulting kinaesthetic changes—caused a decrease in the reliability of the responses which may possibly be associated with a decrease, also, in the validity; though attempts were made to eliminate this by taking additional readings at these points. In the case of Fig. 1(f), moreover, any fairly gross underrating of the density of the filter would cause the curve to move exactly as it has. However, in both figures, the values at the wavelengths before and after these humps have, again, quite good reliability, so that some humps, and particularly those shown in Fig. 1(a), would seem to be generally indicated.

It is important to describe, at this point, one of the special difficulties in this experiment. Namely, the rigid maintenance of the brightness of λ_1 at the proper level for fusion with B(W) throughout an observing session of one to two hours. $B(\lambda_1)$ must be constant in order for the relative values of $B(\lambda_2)$ to have meaning. It was found, however, perhaps due to some fatigue or adaptation process, that $B(\lambda_1)$ occasionally needed slight readjustments, particularly during long uninterrupted observing sessions. But no such adjustment could be tolerated. Hence, although short rest-periods were interspersed, it is not impossible that some irregularities in the data are due to insufficient control of this factor.

Now, looking at the figures once again, the possibly attractive hypothesis that the veiling function would vary inversely with the luminosity of λ_2 regardless of the wavelength of λ_1, fares quite badly. For example, the one curve which we were able to take almost completely through the spectrum [Fig. 1(a) and Fig. 2(a)] exhibits a maximum at 590 mμ and not at 560 mμ as we would expect from considerations of luminosity.

Then, as a counter hypothesis, on the basis of the opposition of colors, we might expect the flex points to vary somehow with the wavelength of λ_1. Consider the case where λ_2 approaches the complementary of λ_1, so that the color of the mixture $[B(\lambda_1)+B(\lambda_2)]$ approaches that of the reference light B(W). Here we might anticipate that the contribution of color differences to the experience of flicker (the chromatic flicker) would be eliminated, or at least modified, so as to change the veiling function at this point. However, the data are unclear on this. Fig. 1(a) [or Fig. 2(a)] peaks at 590 mμ instead of 580 mμ, and Fig. 1(b) peaks

[13] In addition, the mathematical properties of association and of additivity are shown, by inference, not to hold in the flicker-fusion situation for all these cases where λ_2 is sufficiently different from λ_1.

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at 620 mμ instead of 610 mμ—though both these flex points are close. Fig. 1(e) does not flex at all, while Fig. 1(f) peaks at 530 mμ instead of at about 503 mμ. Moreover, without greater theoretical justification than we have at present, we might expect minimum flex points or dips at the complementaries rather than maximum flex points or peaks, that is, greater not less veiling. In other words, we would suggest that the chromatic opposition (to stretch the analogy, the chromatic veiling) might take place in association with a certain exaggerated veiling of luminance (cf. LE GRAND and GEBLEWICZ, 1937; PIÉRON, 1937).

Let us consider Fig. 2. Here is shown the difference between a normal observer and a severely deuteranomalous one. For both λ_1's the deuteranomalous observer (right dominant eye) is more sensitive to the recurrence of flicker than is the normal observer (left dominant eye). This is true right straight through the spectrum. Though great individual differences in sensitivity to flicker are often reported (particularly, such as here, between the sexes)—even between the two eyes of the same observer—it does seem that a difference of 2·00 log units [e.g. Fig. 2(b), from λ_2=560 mμ to λ_2=580 mμ] is somewhat larger than we would ordinarily expect withou. the operation of one or more specific factors. The hereditary difference in color vision might possibly be one. The fact that obs. N was less well trained than obs. D, would operate in exactly this same direction, but were we to assume this to be the sole or major specific factor, then the systematically decreasing difference between the observers at the two ends of the spectrum might be difficult to explain. Otherwise, the import of Fig. 2 is clear, that a veiling function does exist for the normal observer and has, moreover, basically the same general shape as that for the deuteranomalous observer.

Finally, we may examine Fig. 3. Here we show the effect of the over-all brightness level.

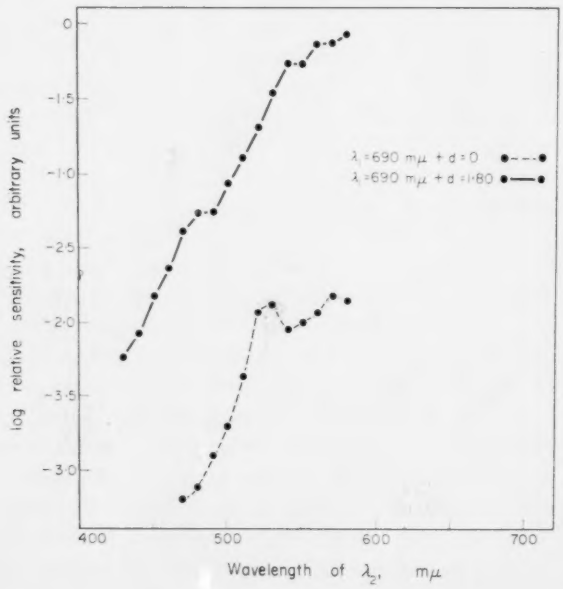

FIG. 3. The veiling functions for a given λ_1 of a severely anomalous trichromate at two different brightness levels: (a) 690 mμ+d=0·00; (b) 690 mμ+d=1·80.

It is positively shown that the magnitude of the veiling function varies directly with over-all brightness level. The mean difference between the two curves is log kI=1·668, which may be

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compared, for example, with the filter density difference of $d=1{\cdot}81$ at 530 mμ. Moreover, the variation in magnitude of the empirical differences between the two curves follows approximately the deviations from neutrality of the transmission curve of the filter used, as we would expect.

SUMMARY

In summary, then, it was found possible to add varying amounts of λ_2 to the flicker-fusion brightness match of λ_1 with white, for $\lambda_2 \neq \lambda_1$, before the flicker reappeared. This amount varied systematically with λ_2 and to some extent with λ_1. Moreover, it varied directly with the over-all brightness level of the $B(W)=B(\lambda_1)$ match. A difference between the normal (♀) and the deuteranomalous (♂) veiling functions was also noted, the deutan subject consistently accepting less $B(\lambda_2)$ than the normal observer.

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EDITOR'S NOTES

THE following international conferences of special interest have been noted:

"Symposium on the Oculomotor System",
Mount Sinai Hospital,
New York City, U.S.A.
14 and 15 March 1961.
Auspices: National Institute of Neurological Diseases and Blindness, U.S. Public Health Service.
Publication is planned.

"Maxwell Colour Centenary",
The Royal Institution and
The Imperial College,
London, England.
16–18 May 1961.
Auspices: The Colour Group; The Institute of Physics and the Physical Society; and the Inter-Society Color Council of the U.S.A.

"Internationale Farbtagung und
Praktische Anwendung Farbwissenschaftlicher Erkenntnisse",
Düsseldorf, Germany.
23–26 May 1961.
Auspices: Fachnormenausschuss Farbe (FNF) im Deutschen Normenausschuss und dem Centre d'Information de la Couleur (C.I.C.) (France); und unter Teilnahme von International Association of Colour Consultants (Paris).
Publication: Special issues of *Die Farbe* and *Couleurs*.

"Conference on Graduate Training for Research in Vision",
University of Rochester,
Rochester, New York.
13–19 August 1961.
Auspices: National Science Foundation, Washington, D.C.

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Beginning with our fourth issue, *Vision Research* will publish critical reviews of important recent books in this field. We would like to call the attention of our readers and of authors and publishers to this service. Books received, but not reviewed, will be listed. Items for such review or notification should be sent to one of the Editors.

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LIST OF ARTICLES TO BE PUBLISHED IN FUTURE ISSUES

TEN DOESSCHATE: Oxford and the revival of optics in the thirteenth century.

WEALE: Further studies of photochemical reactions in living human eyes.

JAY: The effective pupillary area at varying perimetric angles.

FINCHAM: Accommodation and convergence in the absence of retinal images.

BOUMAN and DOESSCHATE: The mechanism of dark-adaptation.

NEGISHI, LU and VERZEANO: Neuronal activity in the lateral geniculate body and the nucleus reticularis of the thalamus.

MARG, MACKAY and OECHSLI: Trough height, pressure and flattening in tonometry.

HEWLETT, PATTERSON, ROBB and SORSBY: Experimental degeneration of the retina—VI. Radiation of the guinea-pig retina.

LENNOX-BUCHTHAL: Single units in monkey (Cercocebus albigena) cortex with narrow spectral responsiveness.

WARD and FRY: An apparatus for the investigation of chromatic adaptation.

WALLS: The evolutionary history of eye movements.

LUCAS: *In vitro* maintenance of the mature guinea-pig retina.

SORSBY, LEARY and RICHARDS: The optical components in anisometropia.

SORSBY and HARDING: Experimental degeneration of the retina—VII. The protective action of the thiol donors against the retinotoxic effect of sodium iodate.

SORSBY and HARDING: Experimental degeneration of the retina—VIII. Dithizone retinopathy: its independence of the diabetogenic effect.

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ERRATA

THE name of Professor H. M. Burian, Iowa City, U.S.A., was inadvertently omitted from the Editorial Advisory Board in the first issue. The Editors wish to apologize for this error.

R. A. WEALE: Notes on the photometric significance of the human crystalline lens. (*Vision Research* **1**, 183–191.)

Please note the following correction to the caption of Fig. 7 (p. 190): For "foveal" read "parafoveal".

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Vision Res. Vol. 1, pp. 313–342. Pergamon Press 1962. Printed in Great Britain.

OXFORD AND THE REVIVAL OF OPTICS IN THE THIRTEENTH CENTURY

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(*Received 15 August 1960*)

Abstract—Three Oxonian scholars, R. Grosseteste, R. Bacon and J. Peckham, are the initiators of the Revival of Optics in the thirteenth century. Their work is discussed.

Résumé—Au cours du treizième siècle trois savants d'Oxford—R. Grosseteste, R. Bacon et J. Peckham—ont fait renaître l'étude de l'Optique.

Zusammenfassung—Drei Gelehrte, die in Oxford lebten, haben im dreizehnten Jahrhundert das Studium der Optik zu neuem Leben erweckt. Es waren Robert Grosseteste, Roger Bacon und John Peckham.

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INTRODUCTION

THREE Oxonians played a leading part in the Revival of Optics in the thirteenth century. The first was ROBERT GROSSETESTE. After him came ROGER BACON and JOHN PECKHAM.[1]

A fourth writer on Optics of the same century was Vitellio (Witelo, Vitello), who was of Thuringian and Polish origin. He never visited England, yet, as will be shown later, it seems possible that the writing of his long treatise does in fact bear a connection with Roger Bacon's *Perspectiva*.

The revival of Optics was part of a widespread movement which started with the so-called Carolingian Renaissance[2] and lasted, though not uninterruptedly, into the thirteenth century. In this century, a gradually increasing number of classical Greek and Arabic books on science reached Western Europe in Latin translations, exerting a vigorous influence.

The reason why the authors mentioned above took such a lively interest in Optics was that they were "Light Metaphysicians". In some very old religious and philosophical doctrines, Fire and Light had been regarded as the main essences of the Universe. Through Manichæism and Neo-Platonism, with its principle of emanation, this idea developed in the course of the early Middle Ages into a philosophical system which Clemens Bäumker called "Lichtmetaphysik". Light was not regarded merely as a symbol, used to indicate the Supreme Being, but as the Essence of the Universe.[3] Our four authors were strongly influenced by this doctrine.

Their writings also show the influence of another ancient way of thought, namely, "Formalism". Grosseteste and his friends in a sense may be described as being "modern", yet they still remained mediaeval clerics.

ALBERT EINSTEIN has written: "What we have come to learn so far entitles us to the certainty that in Nature the idea of a mathematical simplicity is realized" (or "actualized").[4] This statement evokes associations with the conceptions of many Greek and mediaeval philosophers.

Pythagoras (*fl.* 540–510 B.C.) and his followers held that Number was the Essence of the Universe, and some philosophers were convinced that numbers manifested themselves in celestial and terrestrial phenomena. For them geometry was of the utmost importance. Plato, in his *Timaeus*, ascribed to the four elements the shapes of four of the five regular geometrical solids. It is often difficult to understand whether these philosophers regarded numbers and regular solids as symbols of reality, or just the reverse.

With this formalism was linked a strong belief in teleology. The Creator's aim was to make the Universe as excellent as possible and this had to be achieved by the best and most simple means. PLATO, according to Plutarch, said: "God always geometrizes."[5]

Many mediaeval scholars were convinced that they could detect a simple mathematical foundation in natural phenomena.[6] They readily explained why rays of light are straight lines. Between two points can be drawn only one straight line, whereas the points can be joined by an infinite number of non-straight lines. Therefore the straight line was preferred on the strength of this "singleness". Again vision will suffer a minimal loss of vigour when it proceeds along straight paths.

It was also clear to these scholars why, in the case of specular reflection, the angles of incidence and reflection are equal. In this manner the reflected ray is the shortest possible.

An instructive example of this formalistic way of thinking is given by the ancient conceptions about the form and size of the visual field.

According to modern text-books of ophthalmology, the field (for each eye) is of irregular shape, and it extends on the temporal side to more than 90° and on the nasal side to about 55°.

The formalistic mediaeval scientists had the preconceived notion that the visual field must have a regular circumference. Heliodorus of Larissa, who believed that vision operated by means of rays issuing from the eyes, said that these rays must find their places within a regular figure, and that this was a cone of revolution having its apex in the eye and subtending an angle of exactly 90°. If this angle were not a right angle, said Heliodorus, it would of course be either obtuse or acute. Now innumerable acute and obtuse angles are possible, but there is only one right angle. Therefore, this was the angle preferred by Nature.[7] Moreover, a section normal to the axis of this regular cone is a circle. Here the intention of Nature is also obvious, for of all figures with equal circumference the circle encompasses the largest possible area.[8] Formalism also required coincidence of the apex of the cone with the centre of the eyeball.

The Ancients had a preference for constructions in accordance with preconceived ideas and in many cases did not practise anatomy. Their drawings of the visual organ look more like geometrical diagrams than human eyes.[9]

Similarly, considering the first of our three Oxonians, reasonings along such formalistic lines frequently occur in Grosseteste's writings. It is to Roger Bacon's credit, however, as we shall see, that he does not always approve of them. The belief that the World had been created by the best and simplest means was, nevertheless, still prevalent in the thirteenth century.

A. GREEK AND ARABIC THEORIES OF VISION

As the theories on Vision put forward by Greek and Arabic scientists and philosophers exercised a great influence on the thirteenth-century thinkers, a brief survey of these old doctrines is indicated.

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1. *Greek Theories*

The many theories of Vision upheld by Greek philosophers can be divided into three groups:

(1) the centrifugal theories, based on Emission;
(2) the centripetal theories, based on Intussusception;
(3) Plato's *Synaugeia.*

(*a*) *Centrifugal theories.* The theory that Seeing is brought about by rays proceeding from the eyes is very ancient.

The oldest book extant on geometrical optics is EUCLID's *Optics*,[10] written about 300 B.C. It consists of some sixty theorems preceded by twelve assumptions (or definitions). The following is a translation[11] of some of the assumptions:

(1) Let it be assumed that lines drawn directly from the eye pass through a space of great extent;[12]
(2) and that the form of the space included within our vision is a cone, with its apex in the eye and its base at the limits of our vision;
(3) and that those things upon which the vision falls are seen, and that those things upon which the vision does not fall are not seen.

Euclid does not explain in what manner these rays do bring about Vision. He must have chosen this theory because it lends itself to geometrical operations. Euclid connected, in pairs, object points with image points, as it is done in modern constructions. His theorems deal with the sizes of visual angles under different conditions.

It is not clear how the Ancients conceived the manner in which visual apperception arose by means of these rays issuing from the eyes. HIPPARCHUS (160–125 B.C.) is alleged to have said that the rays touched the objects seen like feeling hands.[13] ARCHYTAS of Tarent (*ca.* 430–365 B.C.), a follower of Pythagoras, supposed that seeing was accomplished by *radii . . . oculis profecti sine ullo foris amminiculo. . . .*[14]

The theory of Emission was based on the following facts:

(1) The eyes show a reflected image of the visible objects.
(2) A man who rapidly moves his eyes sees light (phosphenes) even in complete darkness.
(3) Pressure on the eyeball also causes such phosphenes.
(4) Some men (e.g. the Emperor Tiberius, according to SUETONIUS)[15] and many animals can see in dark surroundings.
(5) The eyes of animals often shine and seem to emit light, etc.

The belief that the eye can emit light was very tenacious. In *Henkes Zeitschrift für gerichtliche Medizin* (1833, 4 Quart., p. 266) a legal case is mentioned. A man who was attacked in utter darkness maintained that he had recognized his assailant by means of the light which was produced by a blow with a fist on his eye. Medizinalrath Seiler stated before the judge that this could have been so.

The origin of modern optics goes back to this work of Euclid's.

The most interesting book on Optics written by a scientist of the classical period is PTOLEMY's *Optics* (*ca.* A.D. 150).[16] It is known only through a very poor Latin translation.[17] The first and the last part of it are lost. Thus it is not possible to determine exactly the extent of Ptolemy's knowledge of this branch of science. Consequently it is possible that certain passages in Alhazen and in our thirteenth-century authors, which appear original to us, were in fact borrowed from Ptolemy.

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Ptolemy, like Euclid, accepted the theory of Emission. It is not clear what part Light plays in his doctrine. He was one of the few scientists of the Antiquity who performed purposeful and accurate physical experiments.[18] His observations about double images in binocular vision are excellent.

Most interesting is the manner in which he measured angles of refraction. These experiments of Ptolemy had a great influence on the Oxonians of the thirteenth century, and his results were not surpassed until the seventeenth century. He knew that the path of the rays in refraction is reversible. Table 1 shows the results of Ptolemy's experiments on refraction.

TABLE 1. TRANSITION OF LIGHT FROM AIR INTO WATER

Angle of incidence	Angle of refraction according to Ptolemy	Angle of refraction computed for $n=1{\cdot}3$
0°	0°	0°
10°	8°	7° 29′
20°	15° 30′	14° 51′
30°	22° 30′	22° 1′
40°	29°	28° 49′
50°	35°	35° 3′
60°	40° 30′	40° 30′
70°	45° 30′	44° 48′
80°	50°	47° 36′

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The position of a virtual image produced by refraction was determined by reasoning *per analogiam*. In the case of reflection by a plane mirror, the eye E (Fig. 1a) sees the reflected image of the object V at the point of intersection of the ray EC with the perpendicular VB which falls from V upon the surface of the mirror.[19] Ptolemy knew, furthermore, that a ray of normal incidence is not refracted, and, in determining the position of the virtual image produced by refraction, he also made use of this perpendicular (Fig. 1b). The eye O, which

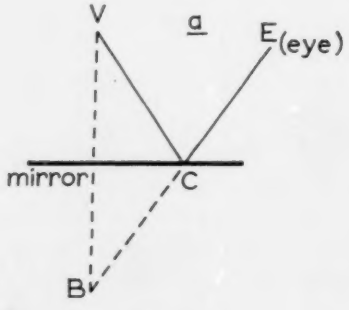

FIG. 1(a)

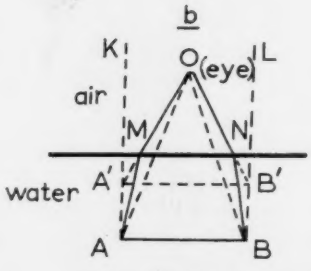

FIG. 1(b)

is in air, looks at the object AB, which is below the water-level. The rays OM and ON are refracted at the surface of the water at the points M and N, reaching the extremities of the object along the paths MA and NB. According to Ptolemy the virtual images of the extremities A and B are determined by protracting the rays OM and ON until they meet the perpendiculars AK and LB. So the virtual image is A′B′. It is magnified because the eye

perceives it under the visual angle A′OB′ which is larger than the angle AOB under which the object would be seen if it were also surrounded by air.[20] Alhazen, Grosseteste, Bacon and Peckham also used this construction. It was ISAAC BARROW (1674) who showed that it is incorrect.[21]

As a psychologist, Ptolemy is, in a sense, a precursor of John Locke, George Berkeley, Hermann von Helmholtz and many other scientists. In his theory the factor "association" takes a preponderant part. When we receive fresh visual impressions we connect them with impressions previously received. We recognize objects as belonging to certain classes which we know by experience. The connection takes place subconsciously by means of syllogisms which are formed so quickly that we are not aware of them.[22] This is essentially the same as HELMHOLTZ's concept of *Unbewusste Schlüsse* (subconscious syllogisms).[23]

It is obvious that such conclusions will sometimes be drawn from defective premises and be false. Here lies the origin of optical illusions. These do not result from defects of the visual organ, but from defective reasoning. Alhazen, Grosseteste, Bacon, Peckham and Vitellio adopted this psychological doctrine.

(*b*) *Centripetal theories.* The theory of intussusception was first put forward by such materialist philosophers as Democritus (d. 361 B.C.) and Epicurus (342–270 B.C.). The Latin poet Lucretius (95–52/51 B.C.) describes it thus: "I say, therefore, that semblances and thin shapes of things are thrown off from their outer surface, which are to be called, as it were, their films or bark, because the image bears a look and shape like the body of that from which it is shed to go on its way."[24]

The following arguments were put forward to support the theory of Immission or Intussusception:

(1) A bright light causes an after-image.
(2) A bright light makes a dim light invisible.
(3) The perceived colour of an object is dependent on the colour of the light which illuminates that object.
(4) Light causes contraction of the pupil (this fact, however, was known only to a few scientists).

Avicenna said that, if the theory of Emission were true, a man with weak eyes (emitting only dim light) would see more clearly when another man with good eyes looked at the same object and that two men would have a higher visual acuity when they both looked at the same time at the same object.

Aristotle (384–322 B.C.) also was an adherent of the theory of intussusception but his conception of the visual process is less materialistic and more difficult to understand. Roger Bacon developed this theory. It is described by the Stagirite himself in the following manner:[25] "The thing seen is . . . colour, and this lies on the surface of the object in itself. Every colour can produce movement in the 'transparent' in a state of activity. Therefore nothing is visible without light. . . . We must explain what light is. Transparency evidently exists. By transparency I mean that which is seen, but not directly seen without qualification, but as it were owing to a colour from somewhere else. The transparent character is shared by air, water and many solid objects. . . . Now *light is the activity of this transparency qua transparent. Potentially*, wherever it is present, *darkness* is also present. *Light* is then in a sense the *colour of the transparency*, whenever it becomes *actually transparent, owing to fire* or any such agency as the upper firmament . . . darkness is a removal of an active condition from the transparency, so that obviously light is the presence of such an active trans-

parency. . . . The colourless is receptive of colour. . . . The *essential nature of colour is its capacity to produce movement*[26] . . . *the actuality of the transparency is light*[27] . . . colour moves the transparency, e.g. the air, and the *sense organ* is moved by this provided that it is continuous."[28]

It seems that Aristotle supposed that in the transparent or "diaphanous" medium surrounding an object, the qualities of that object were present in a slumbering condition from which they were awakened when the diaphanous medium was illuminated by the presence of fire. Then the potential qualities became actual qualities. The process of actualization was propagated from the objects towards the eye, which, being transparent itself, could also manifest the qualities of the visible object. This doctrine did not lend itself as well to geometrico–optical operations as EUCLID's theory.[29]

(*c*) *Plato's* Synaugeia. PLATO's (429/28–347 B.C.) theory, *Synaugeia*,[30] may be regarded as a kind of compromise between the two foregoing ones. *Synaugeia* means coalescence of rays. The following is a translation[31] of parts of Plato's own formulation of his doctrine: "Of the organs first they (the creative powers) wrought *light-bearing eyes*. . . . That part of fire which has the property of not burning, but of yielding an innocuous light, they contrived to fashion into a *substance homogeneous with the light of day*. For the fire within us, being twin with this, they caused to flow through the eyes in its pure form smooth and dense . . . and to filter forth only such fire. . . . Whenever there is daylight around the visual current (the light which flows out of the eyes), this current, issuing from the eyes and meeting with its like, and becoming compacted into union with the latter (i.e. with the homogeneous external daylight), coalesces with it into one homogeneous whole in the line of vision, i.e. in the direction in which the current issuing from within meets front to front with, and presses against, any of the external objects with which it comes into collision."

This theory does not, any more than Aristotle's, lend itself to geometrico–optical treatment.

Goethe sometimes reminds us of this ancient theory: *Wär nicht das Auge sonnenhaft, die Sonne könnt' es nie erblicken. . . .*

Roger Bacon and John Peckham also believed in external and internal rays. They probably knew Plato's ideas on the visual process.

2. *Optics and the Arabs*

During the early Middle Ages the study of science, and therewith of optics, was neglected in Europe. Athens, an important cultural centre, had been the seat of a school where Neo-Platonists still took an interest in physics. But in A.D. 529 the Emperor Justinian disbanded this heathen school and the teachers sought refuge in Asia. During the following centuries Byzantine scholars were more interested in law, history, theology and politics, than in the natural sciences.

The teachers of the disbanded school continued their studies in Persia, Syria and Asia Minor, where many books by ancient Greek philosophers were translated into Asiatic languages. The Arabs, who had conquered the Near East, took a pleasure in science. Many Greek books were translated into their language. Later Sicily and Spain also became centres of culture. The Arabs were not satisfied with making translations. There arose a generation of men who tried to write original works.

About the year A.D. 1000, in Sicily, and even more so in Spain (at Toledo), many books were translated from Arabic into Latin. In the course of time a gradually increasing number

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of these Latin books reached France and England. Scholars in these countries were thus for the first time enabled to get acquainted, although indirectly, with the doctrines of many Greek classical writers. The books aroused enormous enthusiasm and exerted a strong stimulus on the minds of Western scientists.[32]

At first, few of these books were of a high quality. Translating, first from Greek into Arabic, and then from Arabic into Latin, gave rise to many misinterpretations. The very defectiveness of these translations, however, created the urge to obtain better versions.

Euclid, Aristotle (hitherto known only by his book on logic) and Ptolemy became the principal sources from which the scientists in the thirteenth century drew their inspiration. As the Arabs had shown a great interest in Optics and in Ophthalmology, some Arabic authors, especially Alhazen, became very influential in the Western development of Optics. Three other authors are often mentioned, namely PSEUDO-EUCLID, TIDEUS and ALKINDI,[33] but, although they were often quoted by European authors, their works in fact were of no great value. The Arab Alhazen, on the other hand, is a very important scientist who takes a prominent place in the history of Optics,[34] as shown by the following fact. In 1604 the famous astronomer Johannes Kepler published the first modern book on Optics. He gave it the title *Ad Vitellionem Paralipomena*. Now Vitellio, who lived in the thirteenth century, was only a commentator of Alhazen who lived about 1000. This shows that in Kepler's opinion there had been so little progress in the science of Optics, that it seemed to him that his task was merely to add to Vitellio's, and thus to Alhazen's, doctrine.

Alhazen was a man of very wide knowledge.[35] His real name was Abū Muhammed B. Al-Hasen Ibn Al-Haiṭam Al Bāsri. He was a native of Basra (B.C. 962) and he died in Cairo in 1038.

He was a great admirer of Aristotle's. He knew Euclid's *Elements* (but not his *Optics*), Ptolemy's *Optics*, and the works of the physician Galen. He was an eclectic. His treatise on Optics was translated into Latin in the twelfth century by Gerard of Cremona. The first printed edition appeared in 1572. Alhazen had the choice between the centripetal and the centrifugal theory. As a follower of Aristotle he preferred the first[36] and he tried to amalgamate this doctrine with Ptolemy's geometrico-optical theory. From Galen he adopted the idea that the crystalline lens of the eye was the seat of vision.

He taught that sources of light, and objects which reflect or refract rays of light, send forth in all directions pencils of rays which bring along with them "species" or "formae" of the visible objects, as well as colours. His theory was that each separate point of the anterior surface of the crystalline lens, when it is stimulated by a ray, produces perception of a separate point of the visible object. There is thus a distinct connection in pairs between object points and image points.[37] Each perception of a point is accompanied by a distinct sense of direction. This sense of direction of the points of the anterior surface of the lens depends on an innate faculty. Here Alhazen met with a first difficulty, which is illustrated by Fig. 2.

According to Alhazen, stimulation of a point on the anterior surface of the lens gives rise to a perception of a point of light placed along a distinct direction with respect to the eye. Now consider three point-sources of light, *R* red, *B* blue and *Y* yellow, in front of the eye. Every point, *a*, *b*, *c*, *d*, *e*, *f*, *g*, of the anterior surface of the lens receives rays of these three colours. Point *d* receives red, blue and yellow rays, and thus should cause a sensation of a *mixed* colour coming from the direction *dB*. A similar conclusion applies to the case of all the other points. Therefore the result should be the perception of a *homogeneous* visual field of mixed colour, a field devoid of gradients. Such a uniform, empty, field would of

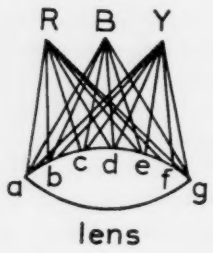

FIG. 2

course be quite useless. It could be compared with that which the Dutch poet Herman Gorter called "a dome of *blind* light" (*een koepel van blind licht*). Hegel already had said: *. . . im reinen Lichte sieht man nichts, . . . erst an der Grenze fängt die Realität an* (*Encycl. d. philosoph. Wissenschaften*, 1817).

Alhazen avoided this obstacle by introducing an abstraction. He assumed that only those rays which are normally incident upon the surface of the lens give rise to a perception of light. To support this hypothesis he mentions the fact that an arrow hitting a target does produce the maximum effect when its direction is normal to the surface of the target. By introducing this hypothesis Alhazen could deal with the subject in accordance with Ptolemy. For whether the direction of the rays was centrifugal or centripetal made no difference to demonstrations on paper. One was dealing only with straight lines, and the correspondence between object points and image points was restored.

On the assumption that only rays normally incident on the lens were effective, it was also necessary to assume that the rays penetrated the cornea along directions normal to its surface, and normal also to the anterior surface of the crystalline lens.

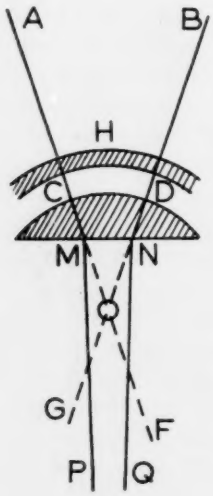

FIG. 3

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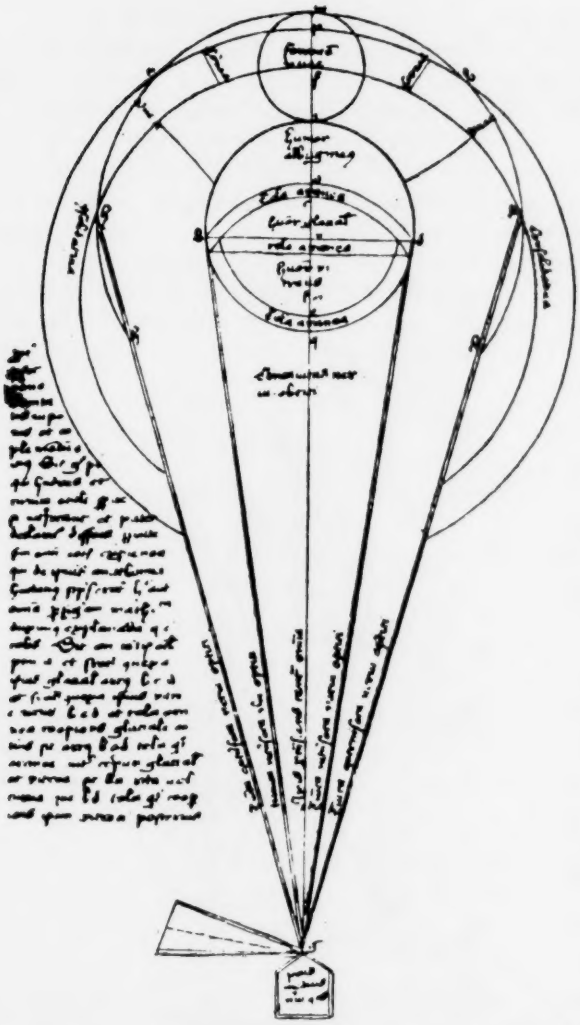

FIG. 4. Anatomy of the human eye, according to VITELLIO (Ms. Bibl. Nat. Paris).

According to Alhazen an object produces impressions on the lenses of *both* eyes, so that it was apparently to be expected that *double* vision would always occur. In order to avoid this further difficulty the author introduced yet another hypothesis.

Alhazen said that vision was not completed at the anterior surface of the lens. From Galen he borrowed the idea that the optic nerves were hollow (*nervi concavi*) (Fig. 3). The normally incident rays pass through the anterior surface of the lens and penetrate into the interior of the eye. Being normal to a spherical surface, they should meet in the common centre of curvature of the cornea and the anterior surface of the lens, at *O*. If such were the case they would continue their course in the directions of *OF* and *OG*, and so the ray

AO, which at first was on the left side, would come to the right side; the opposite would be the case with the ray *BO*. Alhazen could not accept this crossing of rays. For, before KEPLER (1604), no scientist could bring himself to believe in an inverted retinal image. Therefore Alhazen had to change the paths of these rays. He says that they were refracted at the posterior surface of the lens, at the points *M* and *N*, so that they became less convergent. In this manner they were able to enter the hollow optic nerves and reach the point where the two optic nerves meet, the *chiasma nervorum opticorum*. Here the images produced by both eyes eventually coincided, and this explained why vision was not double.[38] This made it necessary for Alhazen to introduce the hypothesis that the lens was less dense than the vitreous body behind the lens.

The chiasma was regarded as the seat of the *Sensus Communis*. In Fig. 4 the pentagon below shows the seat of the Sensus Communis. The eyeball with the optic nerve suggests the idea of a funnel. The figure is very formalistic. All the centres of curvature are on the axis of the eye.

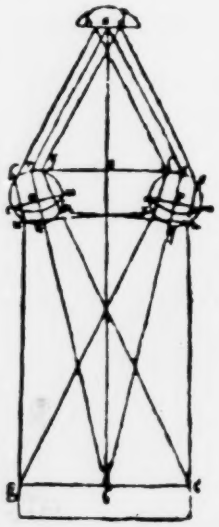

FIG. 5. Binocular vision, according to VITELLIO's *Perspectiva* (1572). RISNER (Editor), Basle (Univ. Libr. Leyde) 676 A 13.

Fig. 5 indicates how the images of three object points, produced in the two eyes, should coincide in the chiasma.

All this may seem rather naïve and it is full of errors. Yet, by reintroducing the centripetal theory of vision, Alhazen showed the right path to future generations of students of optics.

The psychological part of Alhazen's book conforms with Ptolemy's ideas. Alhazen's theory also makes use of subconscious syllogisms. He was a very good observer. Many passages in his work might have been written in the nineteenth century. He repeated Ptolemy's experiments on refraction and made the discovery that incident and refracted rays proceed in the same plane as the normal.[39] Like his predecessors he failed to detect a

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regular relationship between the angle of incidence and the angle of refraction. His method was very accurate. It is a pity that he did not give the numerical results of his experiments.[40]

Alhazen used Ptolemy's (erroneous) construction for the virtual images formed by refraction. His study of refraction was not limited to plane surfaces. He is, as far as we know, the first scientist who mentions refraction by curved surfaces. It is possible, however, that Ptolemy dealt with this subject in the last part of his book, which is lost.

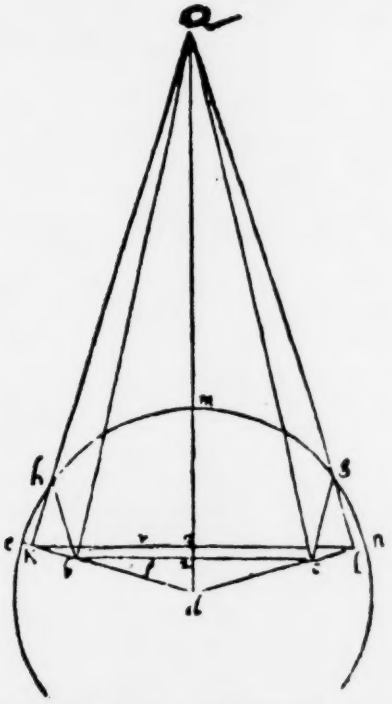

FIG. 6. Magnification of an image by means of a glass sphere. VITELLIO (1572), *Perspectiva*, RISNER (Editor).

Fig. 6 shows the construction of the virtual image produced by one curved surface.[41] The rays *bh* and *cg*, issuing from the extremities of the object *bc*, reach eye *a* after being refracted at *h* and *g*. The lines *ha* and *ga* are protracted. They intersect the normals on the spherical surface (*de* and *dn*) at *k* and *l*. The line *kl* is the virtual image of *bc*.

The virtual image produced by two refractions—in the case of a glass sphere—is also mentioned (Fig. 7). The eye-point is *A* and the object is *bc*. Two rays, *bi* and *bj*, issuing from *b* reach the eye along the paths *bieA* and *bjfA*. Two rays, *ch* and *ck*, coming from *c*, reach the eye along the paths *chdA* and *ckgA*. Rays proceeding from intermediate points of the object *bc* leave the sphere between the points *d* and *e* and between *f* and *g*. The virtual image is situated where the rays *Ad*, *Ae*, *Af* and *Ag* intersect the normals *Od*, *Oe*, *Of* and *Og*. The result is a corona or armilla.[42]

It seems that Alhazen did not perform experiments with lenses or, if he did, his lenses were so imperfect that they did not produce clear images.

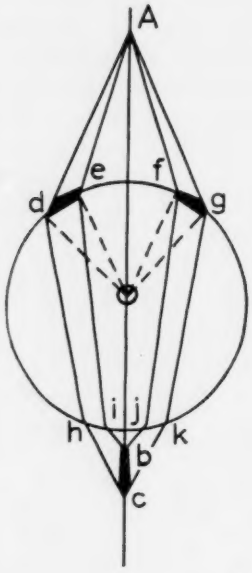

FIG. 7

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B. GROSSETESTE

The new Latin translations of Greek and Arabic texts became known in England, where Robert Grosseteste became interested in optics.

Grosseteste was born in Suffolk about 1175. He studied at Oxford and probably at Paris. After his return to Oxford he became Rector Scholarum, Chancellor and, in 1224, Rector of the Franciscan habit; he was a secular priest. At Oxford he laid the foundation of his knowledge of Aristotle. He was a good Greek scholar and probably wrote a commentary on Aristotle's *Physics*. In 1225 he was elected Bishop of Lincoln. He at once set himself to reform all the abuses which his predecessors had left behind them. He had a very difficult life and was involved in many quarrels. He died in 1253. Probably no one exerted a greater influence upon English thought and literature during the two centuries following his time than Robert Grosseteste. His personal influence during his lifetime was scarcely smaller.[43] He was a great man.[44]

Grosseteste was a Light metaphysician[45] and entered the field of optics by the road of mathematics. The geometry which he required was very elementary, yet it would have been too difficult for scholars of the tenth and eleventh centuries. It was about the year 1000 that Gerbert of Aurillac (Pope Sylvester II, 999–1003) had introduced from the Spanish March the abacus and the new Indian method of computation. Gradually mathematical knowledge spread more and more. Geometry was reintroduced by Adelard of Bath's translation of Euclid's *Elements*. Such a revival of mathematics was needed to enable the study of optics to start.[46]

Roger Bacon says that *apud Latinos* lectures on optics were never held at Paris or anywhere else, except at Oxford. It seems probable that here Grosseteste was the lecturer,

for he was at Oxford and he is the only scholar whose writings on optics have been preserved.[47]

Among his many treatises the following deal with optics:

(a) *De luce seu de inchoatione formarum;*[48]
(b) *De lineis, angulis et figuris;*[49]
(c) *De iride seu de iride et speculo;*[50]
(d) *De colore;*[51]
(e) *De motu corporali et luce.*[52]

According to Grosseteste light is the dominant factor in the World[53] and its most important property is self-multiplication.[54] Light also creates Space.[55]

In his speculations on optics, Grosseteste makes use of the centripetal as well as of the centrifugal theory.

The emanation of light proceeds along straight lines. This is a manifestation of Nature, which always follows the shortest possible ways.[56] The straight line *habet aequalitatem sine angulo: sed melius est aequale quam inaequale.*

That normally incident rays of light produce maximal effect is obvious, because the right angle ranks higher than an acute or obtuse angle.

Speaking about reflected rays, the author says that normally incident rays lose more of their energy than obliquely incident rays, because the alteration of direction (the difference between the incident and the reflected directions) is maximum when the rays are perpendicular.

Reflection on smooth surfaces is stronger than on rough surfaces because in the latter case the species are scattered.[57]

At a surface separating two different media rays can be refracted in two manners:[58]

(a) rays passing from a more subtle into a denser medium are refracted toward the normal erected on the point of incidence;
(b) rays passing from a denser into a more subtle medium are refracted from the normal.

A refracted ray is stronger than a reflected ray because it suffers less deviation.

A ray refracted towards the normal is stronger than a ray which is refracted from the normal.[59] These statements are based upon theoretical considerations and not on experiments and are often inexact.

In *De iride seu de iride et speculo* the word *Perspectiva* is used as a synonym of Optics. *Perspectiva*[60] is subdivided into three parts:

(1) The science of straight rays (*De visu*).
(2) The science of reflected rays (*De speculis*).
(3) The science of refracted rays.

Grosseteste says that this third subdivision had not yet been an object of study in England,[61] but that Aristotle had already written about this difficult topic. Ptolemy and Alhazen he does not mention.

He says that *philosophi naturales* are adherents of the doctrine of Intussusception, whereas mathematicians make use of the centrifugal theory.

Although Aristotle speaks of vision as a centripetal process, there are some passages in his work which, in Grosseteste's opinion, indicate that he also believed in emission. Grosseteste quotes these passages, which are not very convincing, but which enabled him to deal with reflection and refraction according to the centrifugal theory.[62] Why he preferred

this theory is easy to understand. It enabled him to use straight lines and connect object points with single image points.

It seems that Grosseteste did not know Alhazen's and Ptolemy's books or, if he saw them, that he did not study them carefully. Otherwise it might be expected that he would have solved the problem of refraction in a different manner.

His conception in this respect is very formalistic. He was convinced *a priori* that between an angle of incidence and the correspondent angle of refraction there must exist a simple and regular relationship. He reasoned by analogy. In the case of reflection, the angle of incidence and reflection are equal. In refraction this equality cannot exist, otherwise there would be no refraction. The next simple proportion to 1 : 1 is 2 : 1. Therefore: the refracted ray's direction *bf* is the bisectrix of the angle *cbd* between the normal *ed* at the point of incidence and the prolongation of the original direction of the incident ray (Fig. 8).[63]

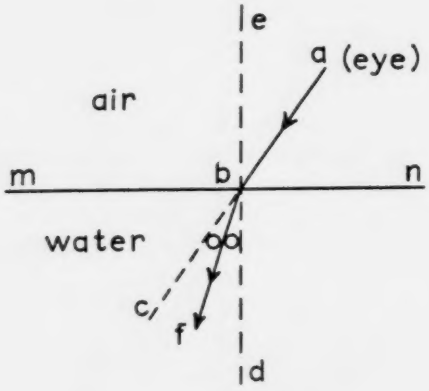

FIG. 8

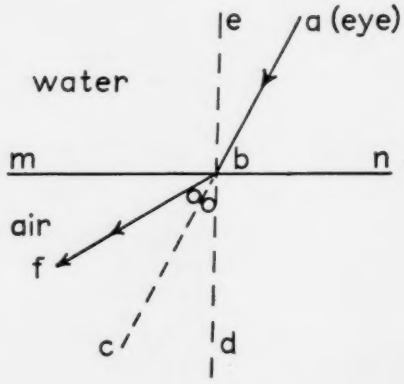

FIG. 9

In this case the eye is situated in the more subtle medium (air). When the eye is surrounded by the denser medium (water) (Fig. 9) the protracted direction *bc* is the bisectrix of the angle *fbd*.[64]

The construction of the virtual image of an object, when the refracting surface is plane, is done in the manner indicated by Ptolemy. The question arises whether Grosseteste had *indirect* knowledge of Ptolemy's assertions. He writes: *Res autem, quae videtur per medium plurium perspicuorum, non apparet esse ut ipsa est secundum veritatem, sed apparet esse in concursu radii egredientis ab oculo in continuum et directum protractum et lineae ductae a re visa cadentis in superficiem secundi propinquiorem oculo ad angulos aequales* [*normally*] *undique* (cf. Fig. 1b). Refraction by curved surfaces is not mentioned. Therefore it seems that Grosseteste did not know Alhazen's *Optics*.

His theory of the rainbow is not original.[65] Rays of light produced by the sun are refracted by the drops of a *hollow* cloud and give rise to the phenomenon.[66] Whereas here he speaks of refraction, however, earlier authors spoke of reflection.

De colore is a very short treatise. Colour is Light incorporated into the *perspicuum* (diaphanous medium).[67] A great deal of bright light in a pure perspicuum is *whiteness*; a dim light in impure surroundings is *blackness*. Between white and black there are fourteen colours.

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In Grosseteste's *De iride* there are two remarkable passages: "For this part of *Perspectiva* [on refraction] shows us by what means we may make very remote objects appear to be quite near, and large objects, which are near the eyes, appear very small, and remote small objects appear as big as we like, so that it is possible for us to read very small characters at an incredible distance or to count grains of sand, or blades of grass or any other very small things."

". . . and it is clear to them in what manner they can shape perspicuous bodies, so that those perspicuous objects receive the rays, issuing from the eye, under a visual angle in the eye, as large as they like, and constrict the rays as much as they like on the visible objects, big or small, far away or near; and in this manner all visible objects may appear in any place and any size *ad libitum*; and it is clear how they can make very large objects appear very small, and, contrariwise, very small and remote objects as if they were big and very well discernible by sight."[68]

It is often said that Roger Bacon was the first scientist who hinted at the possibility of using lenses in spectacles and telescopes, but in this respect the preceding passages show that Grosseteste has the priority.

Did Grosseteste perform experiments with lenses? His inaccurate ideas on the proportion between the angles of incidence and of refraction do not give the impression that he was a great investigator.

Was he a visionary who foresaw the future development of optics? It is possible, though it cannot be proved, that he gained some knowledge from books written by other authors.[69]

Spectacles are first mentioned about the year 1300. Did Grosseteste and Bacon by their visionary utterances stimulate some contemporary to a more accurate study of the properties of lenses, which led to the invention of spectacles?[70] *Non liquet.*

To scientists of today Grosseteste's doctrine may seem naïve, devoid of solid foundation, and possessed of few original ideas. Nevertheless, as a scholar, his attitude differed very much from that of most of his colleagues. In the first half of the thirteenth century he was one of the few men who were really interested in Nature, in mathematics, in optics. At the same time he was a man of wide interests, versed in literature and philosophy.

Grosseteste lived in a century when scholars were convinced that every problem could be solved by metaphysical deduction and when—just as in the first half of the nineteenth century, at the time when the schools of Fichte and Schelling were flourishing—scientific observation of natural phenomena was considered to be a pastime of an inferior and useless kind.

It would be impossible to expect that Grosseteste would at once have become a scientist in the modern sense of the word. But a man of the thirteenth century who preached a doctrine differing to some extent from those of his contemporaries may claim a certain measure of originality. Grosseteste was the first in a very long series of scientists who gradually raised optics to its present level. It was not given to him to take many steps in the goodly land. His writings on optics occupy only a relatively small space (about twenty pages) in his voluminous work.

C. ROGER BACON

As the number of Greek and Arabic books translated into Latin increased, the representatives of the generation following Grosseteste had more and more books of this kind at their disposal. Thus Roger Bacon could become acquainted with the works of Euclid, Ptolemy, Alkindi, Alhazen, Constantinus Africanus, Theodosius and Aristotle. In Bridge's

edition of Bacon's works[71] 212 pages are taken up by his *Perspectiva* and his *De multiplicatione specierum.*

Roger Bacon,[72] the "doctor admirabilis", was born between 1210 and 1215. He studied first at Oxford. His knowledge of Greek and Hebrew later made him independent of bad Latin translations. About 1240 he went to Paris, where he took his doctor's degree. There he made the acquaintance of Adam de Marisco, a man who kept himself far away from the prevailing metaphysical controversies and who, in private, pursued experimental research. It seems that Adam de Marisco exerted a great influence on Bacon.[73]

At Paris, it is likely that Bacon heard about two of his countrymen, Alexander Neckham and Alfred of Sareshel, who had previously lectured there on Aristotle's *Physics*. Between 1245 and 1250 Bacon took the Franciscan habit. He lectured at Oxford between 1250 and 1257.

In 1255 Bonaventura (John Fidanza), an exalted mystic, was elected General of the Franciscans. He disliked suggestions about Church reform put forward by Bacon. Bacon was sent to Paris, where he was put under restraint and for ten years was kept under close confinement without being able to communicate with his friends. In 1268 he was back in Oxford.[74]

Pope Clement IV, who had met Bacon during his visit to England, sent him a letter[75] enjoining him to forward to him secretly and privately any writing he could prepare, notwithstanding all injunctions to the contrary from his superiors. In 1266 and 1267 Bacon wrote his *Opus Majus*, *Opus Minus* and *Opus Tertium* and sent these by a trusted messenger to the Pope. The fate of these manuscripts is not known. Clement, who seems to have evinced a friendly disposition towards Bacon, died on 29 November 1268. Three years elapsed before his successor, Gregorius X (1271–1276), was elected.

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In 1277 Jerome d'Ascoli, who had succeeded Bonaventura, convened a chapter of the Franciscans in Paris. Here Bacon was condemned *propter novitates suspectas*, and he spent fourteen years in prison.[76] Soon after being released he died, in 1292 or 1294. "Greek, mathematics, and experimental science were overwhelmed in the paralyzing mists of Scotian dialectic" (BRIDGES).[77] In the two following centuries there was almost no progress in the domain of optics. The revival had been of short duration. In the thirteenth century mediaeval philosophy was flourishing and scholars turned away from descriptive observation and analysis of empirical facts, applying themselves to metaphysical deduction and to the classifying of ideas.[78]

Alhazen's *Perspectiva* was Bacon's guide in his writings, which to a large extent constitute a commentary on the book of the Arab. Bacon adopted the idea that only normally incident rays are effective and he also accepted Alhazen's psychological doctrine.

Bacon's description of the anatomy of the visual organ is based on Galen, Avicenna, Constantinus Africanus and Alhazen.[79] He too believed that the crystalline lens was the seat of vision and that the act of seeing was completed in the chiasma of the optic nerves.

Whereas Alhazen wrote about convex lenses only, Bacon mentioned also the optical properties of curved surfaces having their *concavity turned towards the eye*. Here he distinguished four different situations (*canones*). This classification (Fig. 10), which was also adopted by John Peckham, is as follows:

(a) The object is in the denser medium:

(1) The eye *R* is somewhere between the concave surface and the centre of curvature *F*.

(2) The centre of curvature is between the concave surface and the eye.

(b) The object is in the more subtle medium:

(1) The eye is between the concave surface and the centre of curvature.

(2) The centre of curvature is between the eye and the concave surface.

The virtual image is determined by means of Ptolemy's and Alhazen's construction.

Propoſitio XI.

Concauitate diaphani denſioris ad oculum verſa, accidit conuerſo illi, quod contingit conuerſa ad oculum conuexitate.

Quando enim oculus eſt in ſubtiliori medio, & concauitas obuerſa oculo, ac oculus intra cẽtrum & rem viſam, imago quidem propinquior videbitur, ſed minor. Idem fit cæteris paribus, quando centrum inter oculum & rem viſam collocetur. Oculo verò exiſtente in denſiore medio, concauitate tenuioris ad oculum conuerſa, ſiue oculus ſit inter rem viſam, & centrum, ſeu centrum inter oculum & rem viſam, apparebit imago remotior & maior: quæ omnia in ſequentibus patent figuris.

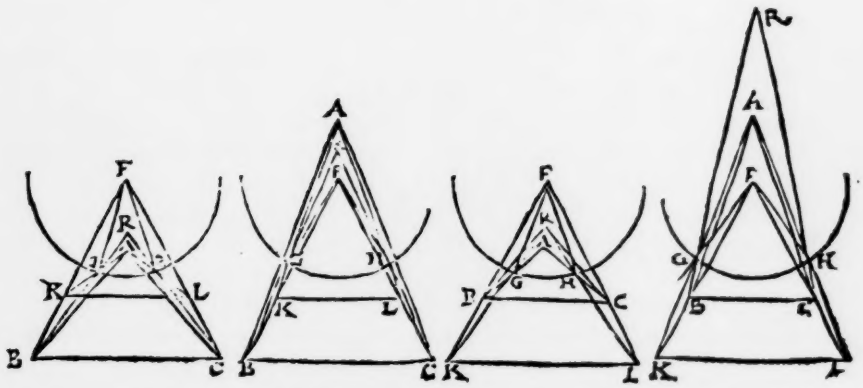

FIG. 10. Formation of images by concave lenses. JOHN PECKHAM (1556) (Editor) (Univ. Libr. Leyde, No. 546).

It is stated by many historians that concave glasses were invented in the fourteenth or fifteenth century, but the idea is already mentioned by Bacon. The question whether or not Bacon's suggestion in this respect was an original one cannot be answered.

Many passages in Bacon's works show that he was a good observer. When he could not prove an assertion by experimental results, he resorted, according to general mediaeval practice, to long and intricate argumentations. He would not have been a scholar of the thirteenth century if he had not sought help in this direction. He was surrounded by colleagues trained in scholastic disputes, who put greater trust in conclusions obtained by means of syllogisms than in visual evidence.

The period was one of system-builders. It was found difficult to accept that anything could be bereft of an explanation. Bacon, in comparison with most of his contemporaries, was a very modest man, who did at times admit that his knowledge was incomplete and that in many cases the use of pure argumentation was insufficient.[80] Other men would have been unhappy without an all-embracing system, and would not have contented themselves with a mere "rhapsody".

Two passages in Bacon's book have attracted the attention of many historians because they seem to prove that Bacon had some knowledge concerning spectacles and telescopes. The following are translations of these passages: "If the letters of a book or any minute objects be viewed through a lesser segment of a sphere of glass or crystal, whose plane base is laid upon them, they will appear far better and larger. Because, by the fifth canon about a spherical medium whose convexity is towards the eye and the object is placed below it and between the convexity and its centre, all things concur to magnify it. For the angle under which it is seen is greater, and its image is also greater, and nearer to the eye than the object itself, because the object is between the centre and the eye. And therefore this instrument is useful to old men and to those that have weak eyes. For they may see the smallest letters sufficiently magnified. But if the medium be the larger segment of a sphere, or but half of one, then by the sixth canon, the apparent visual angle will be greater than the true and the image also greater than the object because the centre of the sphere is between the eye and the object. And therefore this instrument is not so powerful in magnifying as a lesser segment of a sphere. Also instruments made of crystal bodies with plane surfaces, by the first canon about planes, and with concave surfaces, by the first and second canons about spherical surfaces, will perform the same thing. But the lesser of two segments of a sphere magnifies more manifestly than any of them all, by reason of all the three causes. . . ."

The second passage comes from Bacon's *Opus Majus*, and was also translated by Robert Smith: "Greater things than these may be performed by refracted vision. For it is easy to understand by the canons above mentioned, that the greatest things may appear exceeding small and on the contrary; also that the most remote objects may appear just at hand and on the contrary. For we can give such figures to transparent bodies, and dispose them in such order with respect to the eye and the objects, that the rays shall be refracted and bent towards any place we please. And thus from an incredible distance we may read the smallest letters, and may number the smallest particles of dust and sand, by reason of the greatness of the angle under which we may see them; and on the contrary we may not be able to see the greatest bodies just by us, by reason of the smallness of the angles under which they may appear. For distance does not affect this kind of vision, excepting by accident, but the quantity of the angle. And thus a boy may appear to be a giant, and a man as big as a mountain, forasmuch we may see the man under as great an angle as a mountain and as near as we please. And thus a small army may appear a very great one, and though very far off yet very near us, and on the contrary. Thus also the sun, moon and stars may be made to descend hither in appearance, and to appear over the heads of our enemies; and many things of the like sort, which would astonish unskilled persons."[82]

It is small wonder that many (for instance William and Samuel Molyneux and Robert Smith) saw in Bacon the inventor of spectacles and telescopes: "That this learned Frier Bacon who dyed An. 1292, and lyes buried at Oxford, did perfectly well understand all sort of optick glasses, shall be plainly made out, from the natural and easy sense of his own words . . . whereby we shall find, that he not only understood the effects of single convex and concave glasses; but knew likewise the way of combining them, so as to compose some such

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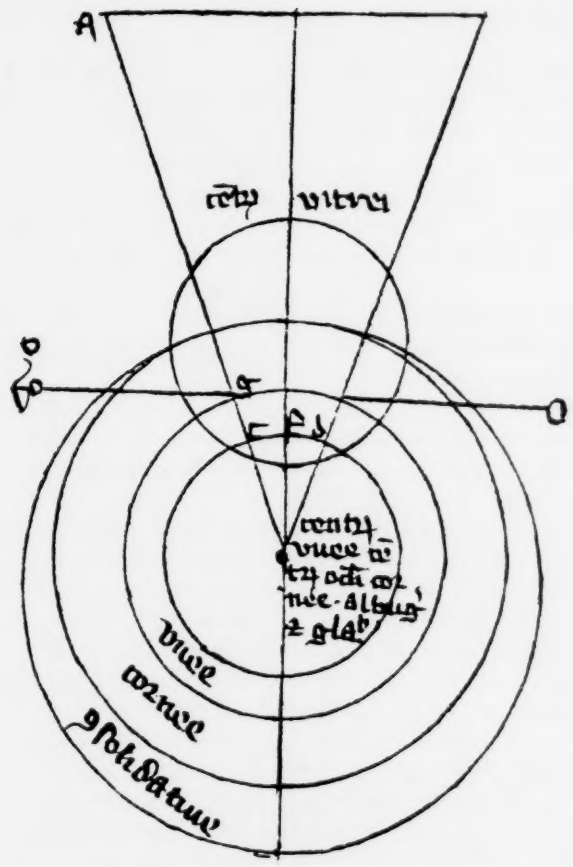

FIG. 11. ROGER BACON, *Perspectiva*. (Ms. Univ. Libr. Prague, No. 1552.)

instrument as our telescope. This perhaps will be looked upon as a great paradox, and as great partiality in an English author to his countryman. . . ."

A comparison with Grosseteste's words, mentioned above, clearly shows that Bacon in this respect was much indebted to his old teacher and friend. That he did not experiment extensively with lenses is apparent from the fact that he sent the Pope a crystal sphere in order to demonstrate its *caustic power*. If he had known spectacles, it should be expected that Bacon would also have mentioned the magnifying power of the sphere—but this he did not mention.

There is a great deal of variation in the illustrations of the several manuscripts of Bacon's optical works. Some anatomical drawings of the visual organ are made with the aid of compasses, others are mere sketchy outlines. A manuscript of the *Perspectiva* in the University Library at Prague (No. 1552) shows a "construction" of the eye reproduced here in Fig. 11. There are three concentric circles which contain between them the words *vuea* and *cornea* (corresponding to the *choroid* and *sclera* of today). A fourth circle, not concentric with the other three, is marked *consolidativa*, the collective name of the components of the

contents of the eye-socket apart from the eyeball itself (fat tissue, muscles, nerves, blood-vessels, eyelids, etc.).[83]

The centre of the three concentric circles is denoted: *centrum vuea*, *centrum oculi*, *corneae*, *albuginei et glacialis*.[84] A fifth circle, intersecting the four others, forms with the inner circle a lunula (similar to the shape of a section through a biconvex lens) and constitutes the posterior surface of the lens and at the same time the anterior surface of the vitreous humour. The words *centrum vitrei* are written at the wrong place. *Umor vitreus* is nowadays called *corpus vitreum* or vitreous humour. The gap between the two horizontal lines indicates the position of the pupillary aperture. The triangle contains all the rays which can enter the eye.[85]

The very interesting treatise called *De multiplicatione specierum* is based on Aristotle's theory of vision and contains, in a sense, a theory from which the modern theory of light could be derived.

Many authors in the thirteenth century wrote about the multiplication of *species*.[86] The word *species* often changed its meaning in the course of time. While the history and development of the doctrine of *species* cannot be discussed here in full, some indications may be given.

In general *species* means something which makes communication between the external object and the visual organ possible. It was used to designate those qualities which are common to the visible object and to the impression which that object makes on the sense organ. In connection with variations in the meaning of the term there came into use synonyms, such as *simulacra*, *intentiones*, *formae*, *spectra*, *similitudines*, *idola*.[87]

For Bacon *species* was the name of the first effect of any natural agent.[88]

According to Bacon, a *species* is not something material, proceeding from the objects towards the eye, like Lucretius's simulacra. He states that if the *species* were material the objects would gradually lose weight and eventually vanish.

He considers the object as an *agens* which incites the perspicuum (diaphanous medium) surrounding it to convert its potential qualities into actual qualities.[89] Thus this medium is the *patiens*.[90] The alteration of the medium (from potentiality into actuality) proceeds from the object, as central point, along all possible directions in straight paths. Therefore it takes some time before the action of the object can reach the eye. But this interval is so short that it is imperceptible.

The action of the object evokes a reaction from the *perspicuum patiens*; the effect of this reaction is the actualization of slumbering properties.

Some authors stated that *species* were of a spiritual nature. Bacon does not agree with this.[91] *Species* take their origin from matter and they exert force on matter, but they are not three-dimensional, contrary to the opinion of Alkindi and Alhazen. Bacon says that if *species* have three dimensions it will be impossible for two rays of light to intersect and afterwards to go on following their original separate directions. Two bodies cannot occupy the same place at the same moment. *Species* are latent qualities of the medium which have come into a condition of actuality. A given particle of the medium can, at the same moment, manifest several different qualities.

It is hardly possible to give an adequate idea of this book of Bacon's in a brief exposition such as the present one.

While many problems could be solved by assuming that the propagation of *species* occurred along straight paths, it was difficult to explain how *species* could reach the *sensus communis* in the chiasma without deviations from the straight road. Therefore Bacon

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introduced the hypothesis that in animate bodies rays could follow tortuous paths along the nerves. This happened under the influence of the soul.[92] A visible object, in illuminated surroundings, stimulates the diaphanous medium to actualize its potential qualities. In the medium there are several slumbering qualities, but only the *species* of light and colour affect the eye.

The propagation of *species* from the visible object may be compared with the modern wave-theory. From the object, as centre, the actualization proceeds in all directions along straight paths which cause spherical fronts of actualization.

If several rays, say, red, blue and yellow, meet in one point, one has to assume that the particle of the medium which is at that moment in that point, actualizes simultaneously its red, blue and yellow qualities.

Because the actualization proceeds from particle to particle, it might have been expected that wind, blowing transversely, would impede the straight progression of the rays. But this does not occur. The *species* actualized in a specific particle of the medium is not permanent but is continually renewed. When wind removes a particle its place is taken by another particle, which in its turn actualizes the same quality. Thus the actualization is connected with the properties of space, in this case the direction of the straight ray, rather than with the particles which happen to lie somewhere along that line of direction.

In dark surroundings, according to this theory, one might have expected to see between a source of light and an illuminated wall a continuous connecting bundle of light. Bacon explains that we do not see such a bundle by the assumption that the *species* in the air are weaker than those on the wall. Different substances have different powers in multiplying *species*. In order to support this thesis, Bacon points out that a piece of iron held at some distance from a magnet is more strongly affected by magnetism than the air situated between the magnet and the piece of iron.

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There is a passage in Bacon which is somewhat reminiscent of Plato's *Synaugeia*. Every organ creates *species*[93] and therefore the sense organ also must do this. This is proved by the fact that a man can see the eye of another man; thus the eye does produce *species*.[94]

According to Plato's doctrine of *Synaugeia* the two kinds of light become fused. According to Bacon the *species* coming *from* the eyes do not mingle with those coming from the visible objects, because the *species* coming from the eye are derived from an animated body and thus differ from the *species* which come from inanimate objects.[95] In this respect there is a regression in comparison with Alhazen's theory.

Was Bacon the founder of modern *scientia experimentalis*? His own words give rise to doubt in this respect. In his *Opus Tertium* (c. XIII) he mentions a "remarkable and almost unknown genius" (Bridges). This was Peter Peregrinus of Maricourt (Maharncuria or Mahariscuria—Adam de Marisco—?) in Picardy, who has already been mentioned. "One man I know, and one only, who can be praised for his achievements in science. Of discourses and battles or words he takes no heed: he follows the works of wisdom, and in these he finds rest. What others strive to see dimly and blindly, like bats in twilight, he gazes at in the full light of day, because he is a master of experiment. Through experiment he gains knowledge of natural things, medical, chemical, indeed of everything in the heavens or earth. . . . If philosophy is to be carried to its perfection and is to be handled with utility and certainty, his aid is indispensable. As for reward, he neither receives or seeks it. If he frequented kings and princes, he would easily find those who would bestow on him honours and wealth. Or if in Paris he would display the results of his researches, the whole world would follow him. But since either of these courses would hinder him from pursuing the great

experiments in which he delights, he puts honour and wealth aside, knowing well that his wisdom would secure him wealth whenever he choose. . . ."[96] One of Peter's letters has been published by Libri.[97] It is a great loss that so little is known about this idealistic scientist.

Opinions on Bacon's work as a scientist are very divergent. Some saw in him a genius who invented spectacles and telescopes and predicted the discovery of X-rays. Others regard him as a man more of words than of deeds. His achievement can only be assessed by comparing him with his contemporaries and then the judgment is found greatly in his favour.

One man could not create out of nothing a modern physical laboratory and invent many new methods of experimental research and critical scientific discussion. It is sufficient for Bacon's fame that he acted as a guide showing the way towards a new domain of science. He was a martyr who would not hide his advanced opinions. He was *justus ac tenax praepositi.*

Bacon's so-called prophecy of the discovery of X-rays is founded partly on scholastic reasoning and partly on the myth that a lynx would be able to see a corpse buried under a thick layer of earth. His pronouncements on the possibility of manufacturing spectacles and telescopes were, as has been shown, borrowed from Grosseteste.

Nevertheless it is very much to his credit that, in the thirteenth century, he understood that scholastic argumentation alone was not sufficient to reach the goal which all scholars wished to reach. He was prepared to repudiate authority if the results of observation and experiment were in contradiction with established theories. His knowledge was encyclopaedic. Among his contemporaries Bacon takes a prominent place.

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D. JOHN PECKHAM

During the following centuries John Peckham's *Optics* was the most popular book on this subject. It is said that this book was given the name *Perspectiva communis* because it was in use everywhere.[98] It ran into numerous editions. This work probably was so much in favour because of its conciseness. It is a small book in which Alhazen's theory is explained in about 100 propositions.

Peckham's book was *the* text-book until as late as about 1600. At some universities Music, sometimes even Geometry, was replaced by Optics in the study of the Quadrivium. In 1431 students in Oxford had the choice between Euclid's *Elements* and Peckham's *Perspectiva communis*. Optics had officially become one of the Liberal Arts in the Quadrivium.

John Peckham was born in Sussex (perhaps at Petcham). He studied first at Oxford and afterwards at Paris. He entered the Franciscan Order. About 1230 he came back to Oxford. He was elected Provincial Minister of the English Franciscans and Lector Sacri Palati at Rome. In 1279 he was installed Archbishop of Canterbury. He died in 1292. He was a theologian, a mathematician, a physicist and a very voluminous writer.[99]

Although he adopted Alhazen's theory on vision, Peckham was not, like Grosseteste and Bacon, an admirer of Aristotle's: *Johannem Pechanum . . . Peripateticorum novellae doctrinae semper et ubique repugnavisse nemo est hodie qui ignoret.* (Spettmann, loc. cit., p. XV). He also, as a rule, takes only into account rays of almost normal incidence. Yet he has to admit that oblique rays also can sometimes produce vision. It is difficult to understand how he succeeded in reconciling this with his theory.[100]

According to Peckham water produces magnified images because its surface is spherical.[101]

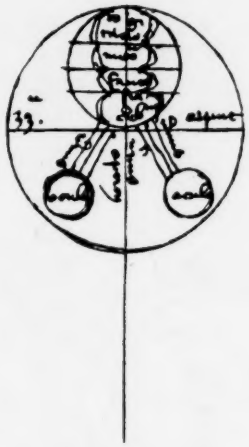

FIG. 12. Anatomy of brain and eyes. JOHN PECKHAM, *Perspectiva communis* (Univ. Library, Basle).

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Our ability to estimate the distance between our eyes and visible objects is based on the fact that we are able to feel the length of the rays coming from the objects.[102]

The same book also contains a great deal of scholastic and inconclusive argumentation. On the whole Peckham's work is less original than Bacon's treatise.

Galen had stated that the brain contained three or four ventricles. Most Arab authors considered that these cavities were the seats of different mental faculties.[103] Bacon and

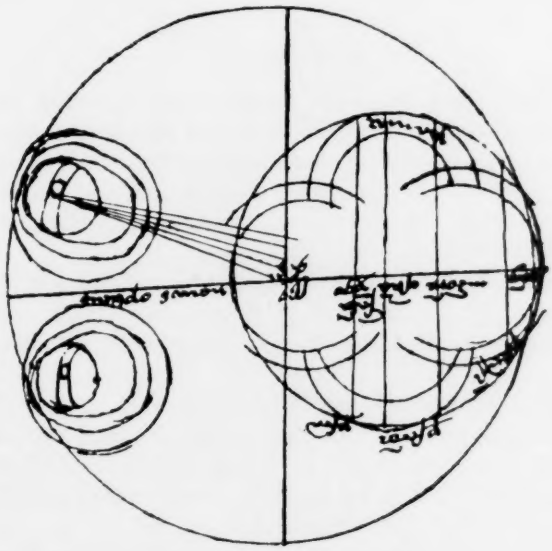

FIG. 13. Eyes and brain, according to JOHN PECKHAM's *Perspectiva communis* (1430). (Ms. by Czechel, Jagellon. Libr. Cracow, No. 1929.)
Inscription: Above: perfectissima, perfectior, perfecta. Middle: cogitativa, memorativa, estimativa, sensitiva imago, sensus communis, nervus opticus. Below: pia mater.

Peckham also accepted this theory. Fig. 12 shows the localization of *cogitacio*, *memoria*, *fantasia*. In Figs. 13 and 14 are shown the seats of *cogitativa* (*scil. virtus*), *memorativa*, *estimativa*, *sensitiva imago*, *sensus communis*. In the printed editions the crystalline lens is drawn in a number of different and fantastic manners.

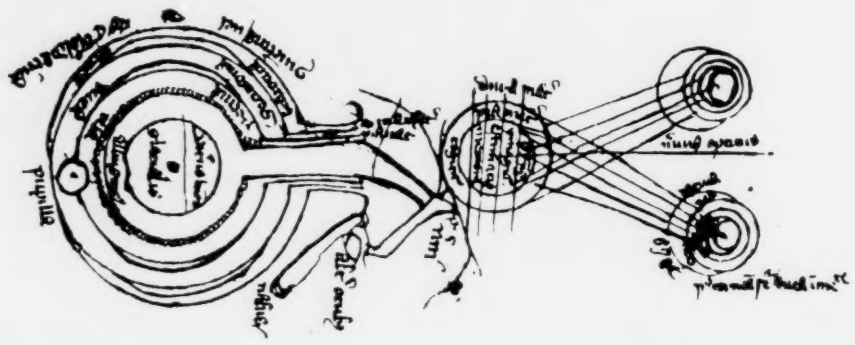

FIG. 14. Eye and brain, according to JOHN PECKHAM (Ms. Nat. Libr. Vienna, No. 5210).

In the process whereby knowledge is obtained about the visible world Alhazen, Bacon, Peckham and Vitellio distinguished two factors, which are nowadays generally called *perception* and *apperception* (*Empfindung* and *Wahrnehmung*, H. von Helmholtz; *Gewaarwording* and *Waarneming*, in Dutch). Light and colour are perceived by means of the *sensus communis* (*solo sensu*).[104] Real understanding of the world depends on other mental faculties, which make apperception possible. Here the role of association and of memory becomes very important.

E. VITELLIO

The most voluminous book on optics written in the thirteenth century is Vitellio's *Perspectiva*.[105] It is little more than a commentary on Alhazen's *Optics*. One of the few additions is a description of perspective phenomena in Euclid's manner.

It is possible, or even probable, that there exists a connection between the books of Roger Bacon and of Vitellio. This hypothesis is based on the consideration of a few facts concerning Vitellio's life.[106]

Vitellio was born about 1230. It is probably that his father was of Thuringian and his mother of Polish origin. Vitellio visited the University of Padua (about 1260). Later he stayed at Viterbo. He was a friend of William of Moerbeke, the Penitentiary of the Papal See.

In the preface of his book, he says that he wrote this work on Optics by special request of van Moerbeke, although he had never before studied this branch of science.[107] It seems that this was a matter of urgency, for he says that in order to complete his task, he left unfinished another book on which he was at work. Vitellio wrote his book about 1270, three years after the reception of Bacon's manuscripts at Viterbo.

All this suggests the following hypothesis: Is it not possible that the ecclesiastical dignitaries at Viterbo—the residence of the Curia—were interested in finding out whether Vitellio, a scholar who was not under suspicion, would pass on Alhazen's optics a judgment similar to Roger Bacon's?

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CONCLUSION

In the three following centuries progress in optics was slow.[108] About the year 1300 spectacles are mentioned for the first time. As these visual aids came more and more into use, there were more occasions to observe the properties of lenses. Otherwise there was almost no progress until the fifteenth century (Porta, Maurolycus and De Dominis). The great obstacle remained: scientists found it impossible to understand how an image inverted on the retina could be compatible with upright vision of the outside world. It was Kepler who, in 1604, removed this obstacle: "Vision, I say, occurs when the image of the whole hemisphere of the external world in front of the eye, in fact a little more than a hemisphere is projected onto the pink superficial layer of the hollow retina."[109]

Robert Grosseteste, Roger Bacon, John Peckham and Vitellio had been the pioneers on the road on which Kepler would earn fame and open up the era of modern optics.

Acknowledgements—Finally, I want to thank Dr. M. H. PIRENNE (Oxford) and Dr. A. C. CROMBIE (Oxford) for their support and very valuable advice.

NOTES

1. "The Oxford school of scholars who reacted against the prevalent methods of logic, philosophy and theology by stressing the study of natural sciences and the languages"; PAETOW, L. J. (1931). *A guide to the study of Medieval History*. The author mentions Grosseteste, Roger Bacon and Adam Marsh. "... dass gerade in Oxford eine Schulrichtung blühte, die wesentlich auf naturphilosophische Probleme spezialisiert war und während Bacons Studienzeit in Robert Grosseteste ihren grossen Professor hatte"; LIEBESCHÜTZ, H. (1932). *Der Sinn des Wissen bei Roger Bacon*, p. 29.
2. RAND, E. K. (1929). *Founders of the Middle Ages*, p. 282. Even before the Carolingian period, there had been a few scholars interested in antiquity, e.g. St. Aldhelm (*ca.* 640–709), Doulton near Wells, *fl.* at Malmesbury, who was acquainted with Greek and possibly also with Hebrew; HASKINS, C. H. (1939). *The Renaissance of the twelfth century*.
3. "Deus dicitur lux proprie et non translative", and "substantia habens magis de luce quam alia dicitur nobilior ipsa"; BÄUMKER, C. (1908). *Witelo, ein Philosoph und Naturforscher des dreizehnte Zahrhunderts*, Münster (1908). *Beiträge zur Geschichte der Philosophie des Mittelalters*, **3**, *Heft* 2. According to SIMPLICIUS (sixth century) (*Commentary of Aristotle's Physics*, 142a–143b) PROCLUS (A.D. 412–485) had said, that Space was subtle light. Cf. Hegel, G. F. W., *Encyclopaedie der philosophischen Wissenschaften*, para. 275: "Das Light ist unendliche Erzeugung des Raums."
4. "Unsere bisherige Erfahrung berechtigt uns zu der Gewiszheit, dass in der Natur die Idee einer mathematischen Einfachheit verwirklicht ist."
5. PLUTARCH, *Quaest. conviv.*, Lib. VIII, c. 1: «ὁ θεός ἀεί γεωμέτρει.»
6. "... si enim visus celerrime pervenire debet ad objectum visibile, per rectam feretur lineam, cum haec omnium illarum linearum brevissima est quae ab ipsis duobus terminis comprehendentur"; HELIODORUS of Larissa (*ca.* A.D. 500), Capita Opticorum, Graece et Latine reddita, Pistoria (1758).
7. "Qua propter natura definitum antefert indefinito, utpote melius, ac animantis rationalis magis proprium, videndi potentia in iis, quae ante sunt, maxime operatur"; HELIODORUS of Larissa.
8. "... si visus aliquid recipere debet quam maxime potest ab objecto visibili, in idem proficietur in figura circuli. Demonstratum namque fuit, hunc esse propriorem inter illas figuras et superficies, quae habent aequalem perimetrum"; HELIODORUS.
9. If they had dissected and observed a human eye, they might have seen that the anatomy did not conform to their formalistic conception. But, even if they had dissected eyes, the conviction that their formalistic conception was right would have made them overlook the incongruity. *Vide:* Illustrations (1931). *Sudhoff's Archiv für Geschichte des Medizin*, published by Bednarski, and POLYAK, S. L. (1941), *The Retina*.
10. *Euclidis Optica*, HEIBERG, I. L. (Editor) (1895). Teubner, Leipsig. The same book contains: *Opticorum Recensio Theonis* (Alexandria, *fl. ca.* 378–395), a commentary on Euclid's book. Here we also find the *Catoptrica*; texts of the three books are given with their old Latin translations; ALBERT LEJEUNE (1948). *Euclide et Ptolémée. Deux stades de l'optique géométrique grecque*. Université de Louvain; *The Optics of Euclid* (translated by H. E. Burton) (1945). *J. opt. Soc. Amer.* **35**, 357–372; PAUL Ver' EECKE (1938). *Euclide, L'optique et la catoptrique* (Oeuvres traduites pour la première fois du grec en français avec une introduction et des notes). Desclée De Brouwer, Paris et Bruges.
11. DISNEY, A. N., HILL, C. F. and WATSON, W. E. (1928). *Origin and development of the Microscope*.

12. Euclid's first supposition is: "Ponatur, ab oculo rectas ductas lineas ferri spatio magnitudinum immensarum"; THEON (quoted in Footnote 10) gives the following version: "Supponamus, radios ex oculo secundum rectas lineas ferri inter se distantes." (The translation given here is from Burton (*op. cit.*).)
13. AETIUS, DIELS' *Doxographi Graeci*, p. 404.
14. APULEJUS, *Apologia*, c. XV.
15. SUETONIUS (1907). *Vitae Caesarum* (Editor Ihm). Leipzig.
16. *L'ottica di Claudio Tolemeo, da Eugenio Ammiraglio di Sicilia, scrittore del Sec. XII* (riduta in Latino, sovra la traduzione araba di un testo greco imperfetto) . . . Pubblicate da Gilberto Govi, Torini (1885); LEJEUNE, A. (1956). L'optique de Claude Ptolémée dans la version latine d'apres l'Arabe de l'émir Eugène de Sicile. (Ed. critique et exégétique.) Université de Louvain.
17. "Das Lesen des Werkes ist eine wirkliche Qual"; HIRSCHBERG, J., *Gesch. d'Augenheilk.*, paragr. 95. (It is a Latin translation of an Arabic version of the original Greek text.)
18. "On y voit des expériences de physique bien faites, ce qui est sans exemple chez les anciens"; DELAMBRE, J. B. (1817). *Histoire de l'astronomie ancienne* **2,** 427.
19. ". . . quod res visae in speculis apparent in concursu visus (visual ray) directe protracti et lineae ductae super speculi superficiem and angulos undique aequales (normal to the surface)."
20. Historians disagree on the question whether the Ancients knew of the magnifying power of lenses. Ptolemy, in his experiments on refraction, made use of a cylindrical lens, but he does not mention its magnifying properties. It is possible that in the last part of his book, which is lost, he spoke about refraction by curved planes. GOVI (cited in Footnote 16) writes (p. 36): "La mutilazione di questo quinto libro ci toglie, per ora almeno, ogni mezzo di conoscere con certezza se gli Antichi avessero o non avessero i ventri lenticolari, non bastando a provare che li avessero quello che Tolemeo vi dici dei mezzi terminati da una superficie piana o da una superficie cilindrica. Chè anzi il non parlarvarsi di vasi sferici, nè di porzioni di sfera potre ben quasi assicurarne del contrario." In the early Middle Ages only the caustic effect of lenses is mentioned.
21. BARROW, I. (1674). *Lectiones opticae et geometricae*, etc. London.
22. "Visus utitur diligenti ratiocinatione cum mirabili celeritate et agit haec insensibiliter propter celeritatem suam." GOVI, G. (Editor) (1885). *L'ottica de Claudio Tolemeo*, p. 33. Torino.
23. *Handbuch der physiologischen Optik* (Third edn.) (1910), 3: "Die psychischen Thätigkeiten . . . sind im allgemeinen nicht bewuszte Thätigkeiten, sondern unbewuszte. Sie sind in ihren Resultate einem Schlusse gleich; . . . in ihren Resultaten den sogenannten Analogieschlüssen kongruent" (p. 25).
24. T. LUCRETIUS CARUS. *De Rerum natura*, 4, v. 42–53:
    (42) "Dico igitur rerum effigies tenuisque figuras"
    (43) "Mittier ab rebus summo de corpore rerum,"
    (51) "Quae quasi membranae vel cortex nominatandast,"
    (52) "Quod speciem ac formam similem gerit imago"
    (54) "Cuiuscumque cluet de corpore fusa vagari."
25. ARISTOTLE: *On the Soul, Parva Naturalia, On Breath*. The Loeb classical library, No. 288 (transl. by W. S. Hett [II, VIII]).
26. «κινητικόν εἶναι τοῦ κατ' ἐνέργειαν διαφανοῦς . . . τὸ χρῶμα κινεῖ τὸ διαφανές.»
27. «ἡ δ' εντελέχεια τοῦ διαφανοῦς φῶς ἔστιν.»
28. «τὸ μὲν χρῶμα κινεῖ τὸ διαφανές, οἷον τὸν ἀέρα, ὑπὸ τούτου δὲ συνεχοῦς ὄντος κινεῖται τὸ αἰσθητήριον.»
29. An excellent survey of Aristotle's theory is given by BEARE, J. I. (1906). *Greek theories of elementary cognition from Alcmaeon to Aristotle*. Oxford.
30. TIMAEUS, 45B–46A.
31. (Translated by J. I. BEARE.)
32. Some knowledge of classic Greek literature was also gathered by travellers who visited Constantinople. But such direct information was much less important than information which was obtained indirectly through Arabic and Latin translations.
33. Alkindi, Tideus and Pseudo-Euclid were upholders of the Emission theory. Their books on optics were published by A. A. Björnbo and S. Vogl . . . *Drei optische Werke* (1912).
34. *Opticae thesaurus Alhazeni libri septem nunc primum editi . . . Item Vitellonis Thuringopoloni libri decem de Optica*, a Frederico Risnero, Basileae (1572).
    The original title of Alhazen's book was: *Kitab-al-manazir*.
35. "The greatest Muslim physicist and one of the greatest students of all time"; SARTON, G. (1927–1931). *Introduction to the History of Science*, p. 721. Alhazen was also astronomer, mathematician, physician and he wrote commentaries on Aristotle and Galen.
36. "Visio non fit radiis a visu emissis. . . ." (*op. cit.*, Vol. 1, 23); "Visio fit radiis a visibili extrinsecus ad visum manantibus. . . ." (*op. cit.*, Vol. 1, 14).

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37. "Visus e singulis suae superficiei punctis singula puncta visibilium videt. . . ." (*op. cit.*, Vol. 1, 15).
38. "Utroque visu una visibilis forma plerumque videtur. Istae ergo duae formae extenduntur a duobus oculis et concurrunt in loco concursus duorum nervorum. . . ." (*op. cit.*, Vol. 1, 27).
39. "Radii incidentiae et refractionis sunt in uno plano. . . ." (*op. cit.*, Vol. 8, 5).
40. He did say that the propagation of species in the denser medium was slower than in the more subtle medium.
41. "Si visus sit in continuato diametro circuli . . . visibile vero inter ipsius centrum et visum, ab eodem centro aequabiliter distet; imago videbitur major visibili" (*op. cit.*, Vol. 7, 44).
42. "Si visus, centrum refractivi convexi densioris, et visibile ultra refractivum positum, fuerint in eadem recta linea; imago videbitur corona seu armilla; et major visibili" (*op. cit.*, Vol. 7, 49).
43. *Dictionary of National Biography;* CROMBIE, A. C. (1953). *Robert Grosseteste and the origins of experimental science, 1100–1700.* Oxford.
44. "Solus unus scivit scientias ut Lincolniensis episcopus"—Roger Bacon.
45. "Et species et perfectio corporum omnium est lux."
"Lux vero omnibus rebus corporalibus dignioris et nobilioris et excellentioris essentiae est. . . . Lux ergo est prima forma corporalis."
46. Grosseteste was probably influenced in this respect by Adelard of Bath (twelfth century), who visited Jerusalem and Spain and became acquainted with Arabic books. Adelard translated Euclid's *Elements* from Arabic into Latin. He was interested in Science [*Quaestiones naturales*; MÜLLER, M. (Editor) (1934). *Beitr. z. Gesch. d. Philos. d. Mittelalters*, Vol. 31]. He may also have read ADELARD's "*De eodem et diverso*", the subject of which was the seven Liberal Arts [Ed. H. WILLNER (1903)].
47. Before Grosseteste the importance of optics was mentioned by DOMINICUS GUNDISSALINUS (Gonzáles, Gundisalvo; twelfth century), who, in his *De divisione philosophiae*, devoted thirty-three out of 140 pages to science and mathematics. His views on optics were based on the centrifugal theory; refraction is not mentioned. This part is borrowed, word for word, from ALFARABI's *De scientiis.* Alhazen is not mentioned. (BAUR, L. (Editor) (1903). *Beitr. z. Gesch. d. Philos. d. Mittelalters*, Vol. 4; MSS.: Oxford, Digby 76, C. Christi 86; Cambridge Univ. Libr. H.h. 4.13.)
48. MSS.: London, Bibl. reg. 6 E V, fol. 242.
Oxford, Merton 295.
Oxford, Digby 104, 98 and 220.
49. MS. : Oxford, Laudon Misc. 644.
50. MSS.: Oxford, Digby 190, 104 and 98.
Oxford, Merton 306.
London, Bibl. reg. 6 E V.
51. MSS.: Oxford, Digby 98, 104, 190 and 220.
London, Bibl. reg. 6 E V.
52. MS. : London, Bibl. reg. 6 E V.
53. "Formam primam corporalem, quam quidam corporeitatem vocant, lucem esse arbitror."
54. This "self-multiplication" will be discussed later.
55. "Lux igitur . . . infinities multiplicata materiam similiter simplicem in dimensiones finitae magnitudinis necesse est extendere"; "ea, quae sunt multa esse multa ab ipsius lucis multiplicatione". "Agens naturale multiplicat virtutem a se usque in patiens, sive agat in sensum, sive in materiam. Quae virtus aliquando vocatur species, aliquando similitudo. . . ."
56. "Natural science, Grosseteste taught, is based on mathematics. . . . He used Optics as best adapted to illustrate the prevalence of mathematical law; but the nature of light had a still wider and deeper interest for him. Light is a force or a form of energy which acts by an instantaneous self-expression in all directions from a centre: it is the simplest and most subtle body, the most akin to spirit, the type and symbol of creative mind." LITTLE, A. G. The Franciscan School at Oxford in the thirteenth century: *Archivum Franciscanum Historicum*, Annus IX (1903), p. 803 ff. See also: Die philisophischen Werke des Robert Grosseteste, Bischofs von Lincoln. BAUR, L. (Editor) (1912). *Beitr. z. Gesch. d. Philos. d. Mittelalters*, Vol. 9.
57. ". . . tunc dissipatur species. . . ."
58. "Et haec est dupliciter; quoniam si illud corpus secundum est densius primo, tunc radius frangitur ad dexteram et vadit inter incessum rectum et perpendicularem ducendam a loco fractionis super illud corpus secundum. Si vero sit subtilius, tunc frangitur versus sinistram recedendo a perpendiculari ultra incessum rectum."
59. The author here makes use of the centrifugal theory.
60. The term "perspective", as a synonym of Optics, is already mentioned by BOETHIUS (*ca.* A.D. 500). It supplanted the word Optica. The treatises written by BACON and PECKHAM were named *Perspectiva* (fem. sing. or neutr. plur.). During the Renaissance *Perspectiva* became the name of the art of suggesting depth in works of art, and *Optics* became again the name of the theory of light and vision.

61. ". . . apud nos intacta et incognita usque ad tempus hoc permansit": BAUR, L. (Editor) (1912). *R. Grosseteste. Beitr. z. Gesch. d. Mittelalters*, Vol. 9 (1917), *ibid.*, Vol. 18.
62. Grosseteste also says: "tres dicti sensus, scilicet visus, auditus, olfactus, exeunt ab instrumentis, sicut aqua exit a canalibus." BAUR: *op. cit.*
63. "Dico igitur, quod incessus radii in secundo diaphana est secundum viam lineae dividentis per aequalia angulum, quem continet radius imaginabiliter in continuum et directum protractus et linea a puncto incidentiae radii ad angulos aequos super superficiem secundi diaphani in profunditatem eius ducta." BAUR: *op. cit.*
64. In spite of the fact that these assertions concerning relationships between angles seem based on purely formalistic speculations, the author says that they are corroborated by experiments: "Quod autem sic determinetur anguli quantitas in fractione radii, ostendunt nobis experimenta similia illis, quibus cognovimus, quod refractio radii super speculum fit in angulo aequali angulo incidentiae"; "Omnis operatio naturae est modo finitissimo, ordinatissimo, brevissimo et optimo, quo ei possibile est." BAUR: *op. cit.*
65. "Necesse est ergo, quod iris fiat per frationem radiorum solis in roratione nubis convexae. Dico ergo, quod exterius nubis est convexum et interius illius est concavum." BAUR: *op. cit.*
66. ANAXAGORAS (*ca.* 500 B.C.) spoke about: «ἀνάκλασιν ἀπὸ νέφους πυκνοῦ τῆς ἡλιακῆς περιφεγγείας.» DIELS, C. H. *Vorsokratiker* (2nd ed.), Vol. 1, s.309.
"Stoici, qui sic in nube quomodo in speculo lumen volunt reddi, nubem cavum faciunt et sectae pilae partem [segment of a sphere]; SENECA, L. ANNAEUS. *Quaestiones naturales*, Vol. 1, 8, 4. The Ancient spoke of reflection, Grosseteste of refraction.
67. "Color est lux incorporata perspicuo"; "Lux igitur clara in perspicuo puro albedo est. Luc pauca in perspicuo impuro nigredo est." BAUR: *op. cit.*
68. *De iride seu de iride et speculo*; BAUR, L. (Editor), pp. 74–75: "Haec namque pars Perspectivae (sc. de refractione) . . . Ostendit nobis modum, quo res longissime distantes faciamus apparere propinquissime positas et quo res magnas propinquas faciamus apparere brevissimas et quo res longe positas parvas faciamus apparere quantum volumus magnas, ita ut possibile sit nobis ex incredibili distantia litteras minimas legere, aut arenam, aut granum aut gramina, aut quaevis minuta numerare."
". . . et patens est eisdem modus figurandi diaphana ita, ut illa diaphana recipiant radios egredientes ab oculo secundum quantitatem anguli, quem voluerint, in oculo facti, et restringant radios receptos, quomodocunque voluerint, super res visibiles, sive fuerint illae res visibiles magnae sive parvae, sive longe sive prope positae; et ita appareant eis omnes res visibiles in situ, quo voluerint, et in quantitate, qua voluerint; et res maximas, cum voluerint faciant apparere brevissimas, et e contrario brevissimas et longe distantes faciant apparere magna et optime visu perceptibiles."
69. Is there any connection with SENECA (*Quaestiones naturales*, Vol. 1, 6, 5); "Omnia per aquam videntibus longe esse majora. Literae quamvis minutae et obscurae per vitream pilam aqua plena majores clarioresque cernuntur. . . ."?
70. HEIBERG, I. L. (Editor) *Catoptrica*, p. 287: "Si res aliqua in vas conjecta et tam remota erit, ut non iam cernetur, si eadem distantia manente aqua infusa erit, res in vas conjecta cernetur." Classic authors also repeatedly mention "the broken oar". Did Grosseteste know other facts mentioned by the Ancients?
71. *The Opus Majus of Roger Bacon.* BRIDGES, J. H. (Editor) (1897). 2 vols. (based on Oxford MS. Digby 235).
"Rogerii Bacconis . . . *Perspectiva* . . . opera et studio Johannis Combachii, philosophiae professoris in Academia Marpurgensi ordinarii, Francofurti" (1614), (copied "e vetustissimis membranis in Oxoniensis Academiae bibliotheca").
72. *Dictionary of National Biography*.
73. ADAM de MARISCO ("doctor illustratus"), Grosseteste's assistant and Bacon's friend, was also a Franciscan. He wrote a book on optics: "Inventi sunt enim viri famosissimi, ut episcopus Robertus Lincolniensis et frater Adam de Marisco et multi allii qui per potestaten mathematicae sciverunt causa omnium explicare et tam humana, quam divina sufficienter exponere." (*Opus Majus*, Vol. I, p. 108.)
74. Roger Bacon was more interested than Bonaventura in natural phenomena, but, apart from this, their respective conceptions in general do not give the impression that there was any great disagreement between them. But a difference which seems slight to us may have been regarded as important in the thirteenth century. On the whole it seems that Bacon's "restraint" at Paris was more due to his revolutionary ideas about Church Reform than to his scientific opinions. (BONAVENTURA, *Beitr. z. Gesch. d. Philos. d. Mittelalters*; LUYKX, B. A., Vol. 23; and *ibid.* (1909), Vol. 6, LUTZ, E.)
75. Issued 22 June 1266, from Viterbo, which was the Papal Residence from 1266 till 1271.
76. In 1277 Pope John XXI ordered Stéphane Tempier, Bishop of Paris, to trace the errors in contemporary science. On 7 March 1277 was issued a decree against 277 errors connected with Averröes's doctrine. Bacon was found guilty of repudiation of authority, and also in connection with his belief in astrology. "Hic Generalis frater Hieronymus . . . condemnavit et reprobavit doctrinam fratris Rogeris Bachonis

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Anglici, sacrae theologiae magistri, continentem aliquas novitates suspectas. . . ." (MANDONNET (1911). *Siger der Brabant et l'Averroïsme de trieziéme siècle*, I, p. 245.)

77. Gregorius X's successor was a famous ophthalmologist, Petrus Hispanus (P. Ulyssiponensis, P. Compostellanus). He was born at Lisbon (*ca.* 1215), was elected Pope in 1276 (John XXI), and in 1277 he died at Viterbo. During his short pontificate he did nothing in favour of Bacon. (His "*Liber de oculo*" was edited by M. A. BERGER (1899): *Die Ophthalmologie des Petrus Hispanus*, with a German translation.)
78. Cl. BÄUMKER: *Witelo*, p. 186.
79. Neither Bacon nor Peckham mentions the name of Ricardus Anglicus (died 1252 in London). He wrote an *Anatomy* (Oxford, Cod. Ashmolean. 399), which was not modern, in so far as the latest Arab author he mentioned was Constantinus Africanus. (Der Micrologus-Text der Anatomia Richards des Engländers; K. SUDHOFF, *Archiv für Geschichte des Medizin*, Vol. 19, s.3.)
80. *Opus Majus:* ". . . et ideo nullus sermo in his potest certificare; totum dependet ab experientia. Et propter hoc non reputo me attigisse hic plenam veritatem. . . . (p. 201); ". . . nec ago potui invenire adhuc. . . ." (p. 208); ". . . et nego me in praesenti tractatu de tanta difficultate certificasse" (p. 210); "Protestor tamen quod in tanta difficultate non loquor praecise, sed multum propinque veritati certificandae. . . ." (p. 273).
81. (Translated by ROBERT SMITH (1738). *A Compleat System of Optiks*. Cambridge. Vol. 2, Remarks 113.) ROGER BACON: *Perspectivae Pars tertia:* Dist. 2, p. 157. BRIDGES (Editor): "Si vero homo aspiciat literas et alias res minutas per medium crystalli vel vitri vel alterius perspicui suppositi literis, et sit portio minor spaerae cujus convexitas sit versus oculum, et oculus sit in aere, longe melius videbit literas et apparebunt ei majores. Nam secundum veritatem canonis quinti de sphaerico medio infra quod est res vel citra ejus centrum, et cujus convexitas est versus oculum, omnia concordant ad magnitudinem, quia angulus major est, sub quo videtur, et imago est major, et locus imaginis est propinquior, quia res est inter oculum et centrum. Et ideo hoc instrumentum est utile senibus et habentibus oculos debiles. Nam literam quantumcumque parvam possunt videre in sufficienti magnitudine. Si vero sit portio major sphaerae vel medietas tunc secundum canonem sextum accidit majoritas anguli, et majoritas imaginis, sed propinquitas deest, quia locus imaginis est ultra rem, non ita valet hoc instrumentum, sicut si esset minor portio sphaerae. Et instrumenta planorum corporum crystallinorum secundum primum canonem de planis, et sphaericorum concavorum secundum primum canonem et secundum de sphaericis, possunt facere hoc idem. Si inter omnia portio minor sphaere, cujus convexitas est versus oculum, evidentius ostendit magnitudinem propter tres causas simul aggregatas. . . ."
82. (Translated by ROBERT SMITH (1738). *A Compleat System of Optiks*. Cambridge. Vol. 2, Remarks 113.) ROGER BACON: *Perspectivae Pars tertia:* Dist. 3, p. 165. BRIDGES (Editor): "De visione fracta majora sunt; nam de facili patet per canones supradictos, quod maxima possunt apparere minima, et e contra, et longe distantia videbuntur propinquissime et e converso. Nam possumus sic figurare perspicua, et taliter ea ordinare respectu nostri visus et rerum, quod frangentur radii et flectentur quorsumcunque voluerimus, ut sub quocunque angulo voluerimus videbimus rem prope vel longe. Et sic ex incredibili distantia legeremus literas minutissimas et pulveres ac arenas numeraremus propter magnitudinem anguli sub quo videremus, et maxima corpora de prope vix videremus propter parvitatem anguli sub quo videremus, nam distantia non facit ad hujusmodi visiones nisi per accidens, sed quantitas anguli. Et sic posset puer apparere gigas, et unus homo videri mons, et in quacunque quantitate, secundum quod possemus hominem videre sub angulo tanto sicut montem, et prope ut volumus. Et sic parvus exercitus videretur maximus, et longe positus appareret prope, et e contra: sic etiam faceremus solem et lunam et stellas descendere secundum apparentiam hic inferius, et similiter supra capita inimicorum apparere et multa consimilia, ut animus mortalis ignorans veritatem non posset sustinere."
83. The "consolidativa", having no optical function, had not to be concentric with the other spheres.
84. "Umor albugineus" is a limpid liquid surrounding the lens, the aqueous humour. "Umor glacialis" is the crystalline lens.
85. The whole diameter of the visual field is here less than 60°. In the printed edition (1614) the triangle is equilateral, so that the visual field has an extent of 60°.
86. For example, VINCENTIUS BELLOVACENSIS, *Speculum naturale*: "Lucis ergo sunt proprietates simplicitas et puritas et sui multiplicatio" (Ed. 1624, p. 35).
87. ". . . cum objectum non contingat oculum se ipso, contingit illud per aliquid sui quo tendit ad oculum: et hoc communiter vocatur species intentionalis seu forma rei visibilis; sive illa fiat qualitas quaedam subtilissima, sive lumen reflexum, sive lumen proprium, sive aliud quidpiam tale, quo res visibilis tendit ad oculum"; M. A. DE DOMINIS, *De radiis visus ect.*, p. 8.
88. ". . . primus effectus cuiuslibet agentis naturaliter. . . ." *De multipl. Specierum*, p. 411.
89. "Fit species de potentia activa materiae patientis." BACON: *op. cit.*
90. "Omne agens physice patitur et transmutatur, insimul dum agit, et omne patiens agit." BACON: *op. cit.*
91. According to BACON (*De multipl. Specierum*), this is a confusion of "spiritualis" with "insensibilis" and "immaterialis".

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92. "Sed in medio amimato per virtutem animae dirigitur species secundum exigentiam operationum animae, et quia operationes amimae circa species fiunt in nervis tortuosis, sequitur species tortuositatem nervi propter necessitatem animae. . . ." BACON: *op. cit.*, Vol. 2, c. 2.
93. ". . . omnis substantia corporalis potest facere speciem." Heat, odour and magnetism are also propagated by species. "Quoniam . . . et substantiae viliores quolibet sensu faciunt speciem, necesse est quod sensus faciat." Vol. 2, 424.
94. ". . . quia homo videt oculum alterius sine speculo . . . sed nihil videtur sine specie, et hoc nullus potest negare absolute. . . ." (p. 452).
95. "Species autem oculi est species animati corporis, in qua virtus animae dominatur, et ideo non habet comparationem ad speciem inanimatae rei. . . ." (p. 53).
96. (Translation: J. H. BRIDGES.)
97. Epistola Petro Peregrini de Maricourt ad Sygernum de Fontancourt militem, de Magnete; LIBRI, GUILLAUME (1838). *Histoire des Sciences mathematiques en Italie*, Vol. 2, pp. 487–505. Libri says: ". . . il mérite une place distinguée parmi les hommes qui ont contribué à la gloire de la France."
98. CANTOR, M. *Vorlesungen über Geschichte der Mathematik*, Vol. 2, p. 88: "Peckham's *Perspectiva Communis* wurde in den folgenden Jahrhunderten geradezu Leitfaden für die betreffende Universitätsvorlesungen."
The book was printed as *Perspectiva communis domini Johannis*, etc.: Milan, 1482, Leipsig, 1504, Venice, 1504, Nuremberg, 1542, Cologne, 1508, 1542 and 1627; an Italian edition appeared at Venice. In 1556 the book was printed at Liége under the title: *Perspectiva tribus libris succinctis per Pascalium Hamellium*. There are still further editions.
MSS.: Oxford, Digby 218, 28, 98
Oxford, Bodleian 30
Gymnasialbibliothek, Thorn R 4°. 2.
The author's name has many variants: Patsan, Betsan, Peckham, Pecham, Pisanus, Londoniensis, etc.
99. SPETTMANN, P. H. (1918). *Beitr. z. Gesch. d. Philos. d. Mittelalters*, Vol. 19.
100. Vol. 3, 13, ". . . radii tamen fracti ad hoc valent, ut res, ex concursu utriusque luminis [viz. irrefracted and refracted rays] clarius videtur." "Per radios qui oblique super oculum oriuntur visio vigoratur et ampliatur."
101. "Aqua enim est superficies sphaerica, tametsi nobis propter magnitudinem apparet plana." Vol. 3, 10.
102. "Longitudinem radiorum a visu comprehendi." Vol. 1, 58; this had also been Ptolemy's idea.
103. GALEN, *De Usu partium*, Vol. 10, c. 10.
AVICENNA, *Beitr. z. Gesch. d. Philos. d. Mittelalters*, Vol. 5.
ALFARABI, *ibid.*
AVICENNA, e.g. said: "prima cellula: sensus communis, imaginatio;
media cellula; phantasia, virtus cogitativa et aestimativa;
tertia cellula; memoria; reminiscentia."
104. "Nullam intentionem visibilium, praeter lucem et colorem, solo sensu comprehendi." PECKHAM, Vol. 1, 62.
105. *Vitellionis περὶ ὀπτικῆς id est de natura, ratione et projectione radiorum visus, luminum, colorum, atque formarum, quam vulgo perspectivam vocant*, Vol. 10 (1st ed.) (1535): GEORGIUS TANSTETTER and PETRUS APIANUS (Editoɪs), Norimbergae apud Io. PETREIUM; (2nd ed.) same title (1551), same editors and printer; (3rd ed.) (1572) *Opticae libri decem*, Basileae (together with Alhazen's *Optics* by F. RISNER.)
106. DOESSCHATE, G. TEN (1940). Lorenzo Ghiberti's third commentary in connection with medieval optics. *Thesis* University of Utrecht (in Dutch).
107. ". . . ut hoc laboris tibi placiti onus subirem hisque materiis mihi nondum cognitis animum applicarem."
108. BIAGIO DA PARMA (BIAGIO PELICANI, d. 1416) wrote a large treatise on optics. This is no more than a commentary on Peckham's book. MS.: Bibl. R. Parma, 3572: *Super perspectiva communi dubitationes per magistrum Blaxium de Parma.*
109. KEPLER, J. (1604). *Ad vitellionem paralipomena, quibus astronomiae pars optica traditur*, Vol. 2, p. 168. Francofurti. "Visionem fieri dico, cum totius hemisphaerii mundani, quod est ante oculum, et amplius paulo, idolum statuitur ad album subrufum retinae cavae superficiei parietem."

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Vision Res. Vol. 1, pp. 343–353. Pergamon Press 1962. Printed in Great Britain.

NEURONAL ACTIVITY IN THE LATERAL GENICULATE BODY AND THE NUCLEUS RETICULARIS OF THE THALAMUS[1]

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Abstract—Recordings of neuronal activity from the lateral geniculate body pars dorsalis and the nucleus reticularis of the thalamus were obtained, by means of single and multiple microelectrodes in cats immobilized with flaxedil and maintained with artificial respiration. Comparisons were made between the patterns of activity which occur, in the two nuclei, spontaneously or as a result of visual stimulation with brief flashes of light.

It was found that patterns of activity—spontaneous or evoked—were different in the two nuclei, in terms of frequency of spikes, grouping and temporal distribution of bursts of spikes, average neuronal activity and latency of response. It is suggested that these differences may be related to different pathways carrying the information from the retina to the two nuclei and to differences in the pathways followed by impulses circulating through their neuronal networks.

Résumé—On a enregistré l'activité neuronale de la partie dorsale du corps genouillé latéral et du noyau réticulaire du thalamus, au moyen de microélectrodes simples et multiples, sur des chats immobilisés au flaxedil et maintenus en vie par respiration artificielle. On a comparé les modes d'activité qui se manifestent dans ces deux noyaux, soit spontanément, soit comme résultat d' une stimulation visuelle produite par de brefs éclats lumineux.

On a trouvé que ces modes d'activité—spontanée ou évoquée—différaient dans les deux noyaux en termes de fréquences des décharges, de groupement et de distribution temporelle des bouffées de décharges, de l'activité neuronale moyenne et de la latence de réponse. On suggère que ces différences peuvent être en relation avec des trajets différents du transport de l'information depuis la rétine jusqu'à ces deux noyaux, et avec des différences dans les trajets suivis par les influx qui circulent dans leurs réseaux de neurones.

Zusammenfassung—Mit Hilfe von Einzel- und Vielfachmikroelektroden wurden an Katzen, die mit Flaxedil immobilisiert und künstlich beatmet waren, die Neuronenaktivität des seitlichen Kniehöckers (pars dorsalis) und des Nucleus reticularis des Thalamus registriert. Es wurden Vergleiche angestellt zwischen den Erregungsmustern, die in den beiden Kernen entweder spontan oder als Folge visueller Reize mit kurzen Lichtblitzen auftreten.

Es ergab sich, dass sich die Erregungsmuster—spontan oder provoziert—in den beiden Kernen unterschieden und zwar hinsichtlich der Impulsfolgefrequenz, der Häufung und der zeitlichen Verteilung der Impulssalven, der durchschnittlichen Neuronenaktivität und der Latenzzeit der Antwort. Es ist zu vermuten, dass diese Unterschiede herrühren von verschiedenen Kanälen, welche die Information von der Retina zu den beiden Kernen vermitteln und von Unterschieden in den Wegen, die von den Impulsen verfolgt werden, wenn sie durch das Neuronennetz laufen.

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FROM the point of view of function the thalamic nuclei are classified as specific, associational and non-specific (JIMENEZ-CASTELLANOS, 1949; RANSON and CLARK, 1953). The specific (relay) nuclei receive impulses directly from the sensory pathways and project upon the sensory areas of the cortex; the associational nuclei are not known to receive impulses directly from the sensory pathways, but receive impulses from other thalamic nuclei and project to associational areas of the cortex; the non-specific (diffusely projecting) nuclei are characterized by projections to wide areas of the cortex and by their widespread influence upon cortical activity (DEMPSEY and MORISON, 1942; JASPER, 1949; MORISON and DEMPSEY, 1942; NEGISHI, 1956; STARZL and MAGOUN, 1951; STARZL and WHITLOCK, 1952; VERZEANO, LINDSLEY and MAGOUN, 1953).

Recent investigations have indicated that, though they receive no direct afferents from the sensory pathways, some of the non-specific thalamic nuclei may respond to sensory stimulation: responses can be evoked in the centre median by various modalities of sensory stimulation (ALBE-FESSARD, ROCHA-MIRANDA and OSWALDO-CRUZ, 1959; ALBE-FESSARD and ROUGEUL, 1958; FRENCH, VERZEANO and MAGOUN, 1953; KRUGER and ALBE-FESSARD, 1960). Other studies have shown that the non-specific nuclei may influence the neuronal responses evoked in the cortex by visual stimulation (AKIMOTO and CREUTZFELDT, 1958; CREUTZFELDT and AKIMOTO, 1958; JUNG, 1958, 1959). These data have, thus, suggested that the non-specific thalamic nuclei may be implicated in the treatment and the control of sensory information.

Among the non-specific nuclei, the nucleus reticularis has several distinctive features: it consists of a layer of cells lying between the internal capsule and the external medullary

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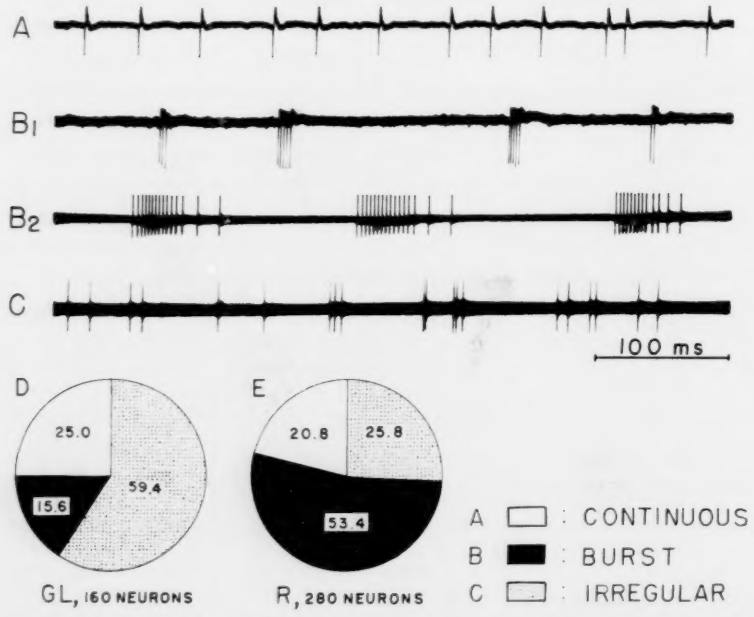

FIG. 1. Patterns of spontaneous activity. A: continuous firing (lateral geniculate); B_1: firing in bursts (lateral geniculate); B_2: firing in bursts (nucleus reticularis); D and E: number of neurons (in per cent of total) which corresponds to the various patterns of activity in the two nuclei (GL = lateral geniculate; R = nucleus reticularis).

lamina and extending from the anterior to the posterior part of the thalamus (RANSON and CLARK, 1953; ROSE, 1952); it is sectionally organized, each section being in close relation to an underlying thalamic nucleus and projecting to a different area of the cortex (ROSE, 1952); its caudal part is in close relation to the lateral geniculate body and has been shown to respond to visual stimulation (NEGISHI and VERZEANO, 1960; VERZEANO and NEGISHI, 1960a).

In order to further investigate the relations between the activity of this nucleus and that of the lateral geniculate body a comparative study of the neuronal activity of the two nuclei has been conducted.

METHODS

Experiments were conducted in cats immobilized with flaxedil and maintained with artificial respiration. Recordings were obtained with microelectrodes made of stainless steel and insulated with an enamel coating. The microelectrodes were introduced into the brain stereotaxically and the location of the recording points was ascertained by serial section and histological preparation (NEGISHI and VERZEANO, 1960; VERZEANO and NEGISHI, 1960a and b).

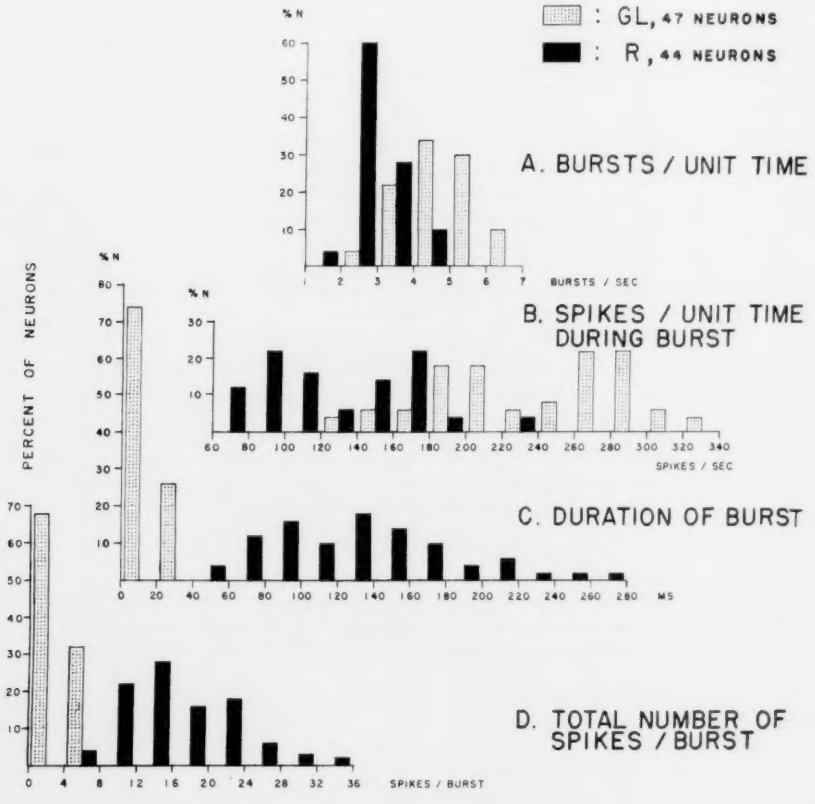

FIG. 2. Comparison of the characteristics of the bursts of spikes which occur, spontaneously, in the lateral geniculate and the nucleus reticularis (see text).

The electronic devices used in this study—amplifiers, oscilloscopes and magnetic tape recorders—were described in previous papers (VERZEANO, 1956; VERZEANO and NEGISHI, 1960a and b). Visual stimulation to the contralateral eye was carried out with brief flashes of light (10 μsec—1000 lux), in dark-adapted animals, with normal pupils. The shape of the pulse was triangular with a rise time of 4 μsec and a decay of 6 μsec, approximately.

RESULTS

A. Spontaneous Neuronal Activity

The patterns of spontaneous neuronal activity which have been found in the two nuclei can be classified as follows: (a) neurons which fire continually (Fig. 1A); (b) Neurons which fire in bursts (Fig. 1B_1 and B_2); (c) Neurons which fire irregularly (Fig. 1C). Fig. 1D and E show the number of neurons whose activity corresponds to each pattern. It can be seen that the neurons which fire in bursts could be found more frequently in the nucleus reticularis.

When the burst patterns are analyzed and compared in the two nuclei it is found that they

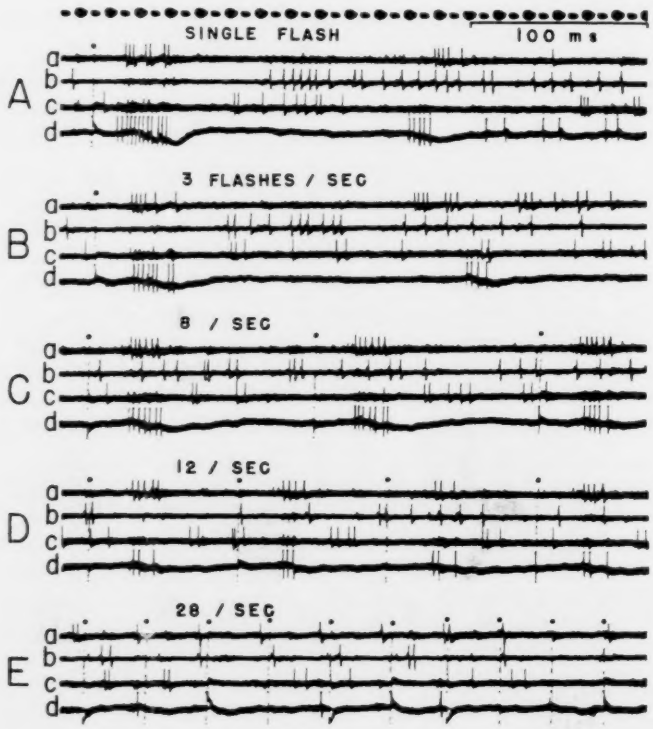

FIG. 3. Responses obtained with four microelectrodes (a, b, c, d) from the lateral geniculate body, by stimulation with brief flashes of light, at various frequencies. As the frequency of stimulation is increased (from A to E), the latencies of response change: the latencies of the neurons recorded by microelectrodes a and d increase; the latencies of the neurons recorded by b and c decrease. The number of spikes per response decreases as the frequency of stimulation increases.

Microelectrodes: a = 2 μ; b = 3 μ; c = 3 μ; d = 2 μ. Distances between tips: a to b = 110 μ; b to c = 130 μ; c to d = 120 μ.

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differ in the following way (Fig. 2): There are more bursts per unit time (A) and more spikes per unit time (B) in the lateral geniculate body; bursts are of longer duration (C) and contain more spikes per burst (D) in the nucleus reticularis. In order to ascertain whether these

TABLE 1. STATISTICAL SIGNIFICANCE OF DIFFERENCES BETWEEN THE BURSTS—PATTERNS OF SPONTANEOUS ACTIVITY ENCOUNTERED IN THE LATERAL GENICULATE AND THE NUCLEUS RETICULARIS

		ΣN	$\overline{X}$	$SE\overline{x}$	T	P
Spikes per burst	GL	735	4	0·6	32·5	<0·01
	R	674	17	0·4		
Duration of burst (msec)	GL	880	20	0·17	28·7	<0·01
	R	664	132	3·9		
Spikes/sec during burst	GL	735	274	4·6	24·3	<0·01
	R	661	143	2·9		
Periodicity of burst (bursts/sec)	GL	649	5·3	0·10	4·88	<0·01
	R	325	4·5	0·13		

Symbols: GL = lateral geniculate; R = nucleus reticularis; N = number of record samples studied; $\overline{X}$ = mean: $SE\overline{x}$ = standard error of the mean; T = T ratio; P = limits of confidence.

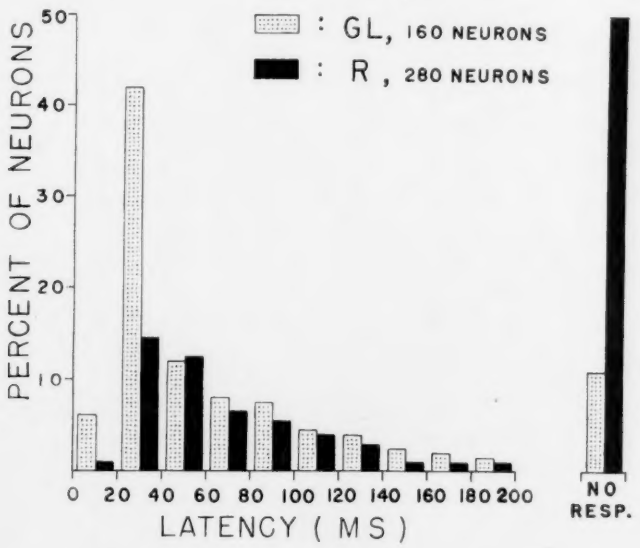

FIG. 4. Frequency distribution of latencies of neuronal responses, evoked by stimulation with a brief flash of light, in the lateral geniculate body and the nucleus reticularis of the thalamus. The columns designated as "no response" represent the number of neurons which showed no response to stimulation.

differences in the burst activity of the two nuclei are statistically significant, the null hypothesis has been tested by calculating the standard error of each difference and applying the "*T*" test. It can be seen from Table 1 that the null hypothesis can be rejected in all cases and, therefore, the observed differences can be considered to be statistically significant.

B. Evoked Neuronal Activity

(1) *Activity evoked with a single flash of light.* When neuronal activity is evoked with a single flash of light and recorded with several microelectrodes (Fig. 3A), it is found that, in both nuclei, various neurons respond with various latencies. Fig. 4 shows the frequency distribution of these latencies and indicates that in most cases the latencies in the lateral geniculate are shorter than in the nucleus reticularis. It has also been found that the latency of the response is related to the intensity of the flash (Fig. 5): latencies of neurons which are,

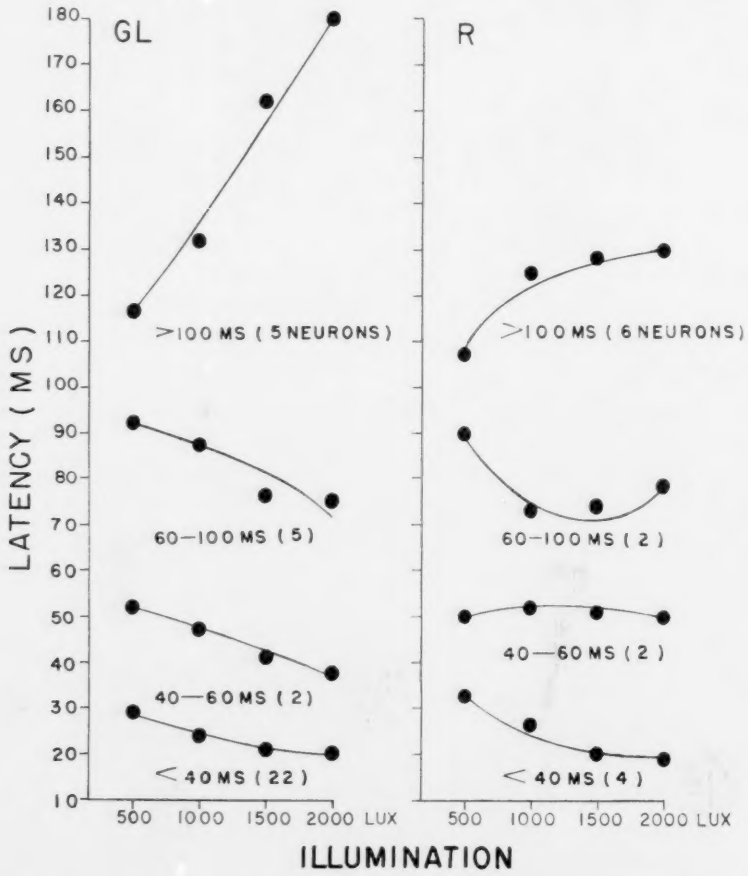

FIG. 5. Latency of response as a function of intensity of stimulus. Left: lateral geniculate body; right: nucleus reticularis. Latencies which are, originally, longer than 100 msec increase as the intensity of the stimulus increases; latencies which are, originally, shorter than 100 msec decrease or remain stationary as the intensity of the stimulus increases. Figures in parentheses represent the number of neurons studied in each category.

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originally, in the 20 to 100 msec range, decrease or remain stationary as the intensity of light is increased; latencies which are, originally, above 100 msec, increase as the intensity of light is increased.

In order to compare the amount and the temporal distribution of the average neuronal activity which occurs, in the two nuclei, after stimulation with a single flash of light, the activity of a number of neurons in each nucleus has been studied in the following way: A period of 200 msec before and 500 msec after the stimulus was divided into 20 msec sections. The frequency (f, spikes/sec) of the impulses generated by each neuron was determined in each 20 msec section. By taking the sum of these frequencies for all the neurons in that section and dividing by the number of such neurons ($\Sigma f/N$), the average activity in each section was estimated. The results, for the two nuclei, are plotted in Fig. 6. They show that, in the 200 msec preceding the stimulus, the average activity is slightly lower in the nucleus reticularis. After the stimulus, there are differences in the events which occur in the two

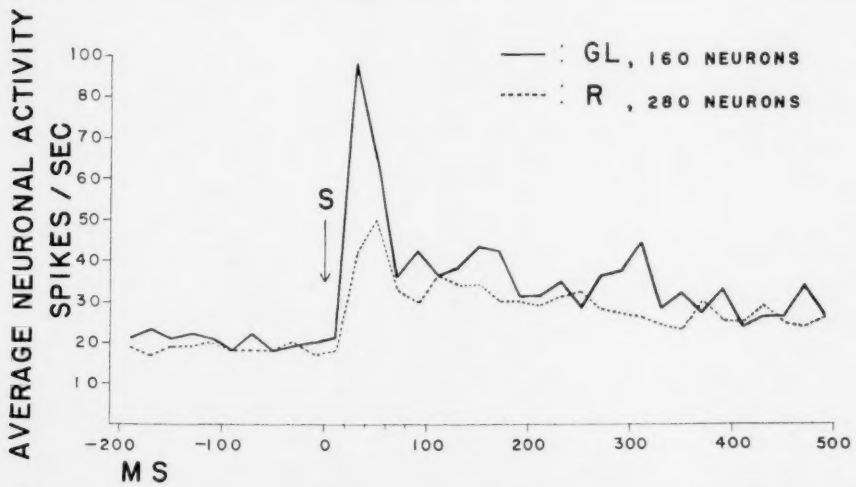

FIG. 6. Comparison of the average activity ($\Sigma f/N$) following a stimulus (S) in the lateral geniculate body and the nucleus reticularis (see text).

nuclei: in the lateral geniculate body the average activity reaches a maximum (about 100 spikes/sec) at 20 to 40 msec, then decreases (to about 37 spikes/sec) at 60 to 80 msec. After this, the activity declines more slowly with small oscillations. In the nucleus reticularis, the activity reaches a maximum (about 48 spikes/sec) at 40 to 60 msec then decreases (to about 30 spikes/sec) at 80 to 100 msec. After this, it declines similarly to the activity in the lateral geniculate body, but with smaller oscillations. Thus, the increase in average activity, after the stimulus, is less marked and occurs later in the nucleus reticularis.

(2) *Activity evoked with repetitive flashes.* Changes in latency and changes in the frequency of spikes have been studied in their relations to the frequency of stimulation (Fig. 3B to E, and Fig. 7). It has been found that latencies of neurons which are originally in the 20 to 60 msec range increase as the frequency of stimulation is increased; latencies which are originally in the range above 60 msec decrease as the frequency of stimulation is

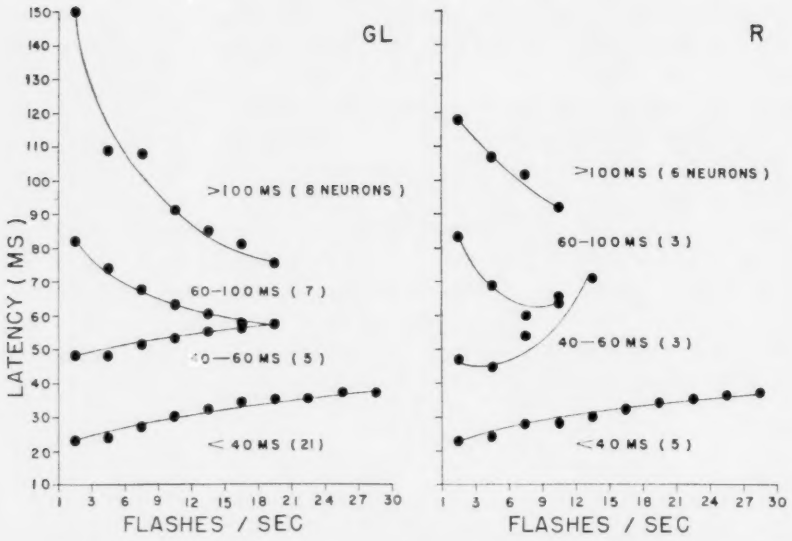

FIG. 7. Latency of response as a function of frequency of stimulation. Left: lateral geniculate; right: nucleus reticularis. Latencies which are, originally, longer than 60 msec, decrease as the frequency of stimulation increases; latencies which are, originally, shorter than 60 msec, increase as the frequency of stimulation increases.

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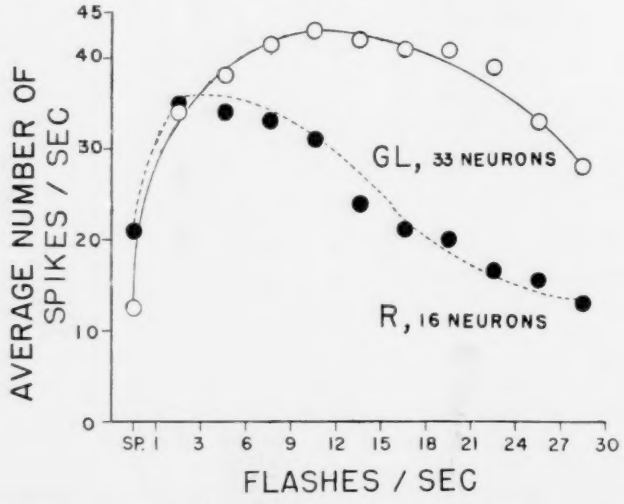

FIG. 8. Frequency of neuronal impulses as a function of frequency of stimulation (see text). Sp.: frequency of neuronal impulses in spontaneous activity.

increased (Fig. 7). The frequency of the spikes increases at first, then decreases progressively as the frequency of stimulation is increased (Fig. 8). In the nucleus reticularis the maximum frequency of the spikes (about 35/sec) is reached at a frequency of stimulation of about 1 to 3 flashes/sec; in the lateral geniculate body the maximum frequency of the spikes (about 43/sec) is reached at a frequency of stimulation of about 9 to 12 flashes/sec (Fig. 8).

DISCUSSION

The neuronal activity of the two nuclei investigated in this study showed similar as well as distinctive features.

The similar features were: (a) in both nuclei the spontaneous neuronal activity showed three types of pattern: continuous activity, burst activity and irregular activity; (b) in both nuclei the latencies of the neuronal responses were related to the frequency and the intensity of stimulation. The changes in the latency of the neuronal response with changes in the intensity of the stimulus, which were observed in the lateral geniculate, were similar to those observed by ERULKAR and FILLENZ (1960) in the same nucleus and by GRÜSSER and CREUTZFELDT (1957), GRÜSSER and GRÜTZNER (1958) and GRÜSSER and RABELO (1958) in the retina and in the visual cortex; those which were observed, in this study, in the nucleus reticularis followed very similar courses; (c) in both nuclei the frequency of the spikes in the neuronal response was related to the frequency of stimulation.

The distinctive features were, mostly, quantitative: (a) the predominant type of spontaneous neuronal activity consisted of bursts in the nucleus reticularis and of irregular activity in the lateral geniculate; (b) the bursts of spikes, when present, were shorter and contained fewer spikes in the lateral geniculate. Some of the characteristics of such bursts in the lateral geniculate were also described in other studies (ERULKAR and FILLENZ, 1960; HUBEL, 1960; VERZEANO, 1955); (c) the changes in the frequency of the spikes in the neuronal response with changes in the frequency of stimulation which were observed in the lateral geniculate body, were similar to those observed by GRÜSSER and CREUTZFELDT (1957), GRÜSSER and GRÜTZNER (1958) and GRÜSSER and RABELO (1958) in the retina and the visual cortex of the cat and by DE VALOIS (1958) in the lateral geniculate of the monkey. The present study shows that, while such changes do obtain in the nucleus reticularis, the maximum frequency of the spikes in the response occurs, in this nucleus, at a stimulation frequency of 1 to 3 flashes/sec as contrasted to the frequency of about 10 flashes/sec which gives the maximum frequency of spikes in the responses of the other structures.

Summing up, the neuronal activity of the caudal part of the nucleus reticularis is characterized by a particular type of burst activity, by latencies of response longer than those of the lateral geniculate and by a maximum frequency of spikes in the response occurring with a stimulation of 1 to 3 flashes/sec.

While the present study suggests that information from the retina does arrive in the caudal part of the nucleus reticularis, it provides no indication as to the pathways over which it is transmitted. The existence of connections between the lateral geniculate and the caudal part of the nucleus reticularis has been suggested in other studies (CHOW, 1952) and may be implicated in these phenomena. However, the latencies of the responses observed, in this study, in the nucleus reticularis, are such that transmission of impulses from the retina by other pathways, involving other non-specific nuclei (HANBERY, AJMONE-MARSAN and DILWORTH, 1954; HANBERY and JASPER, 1953), cannot be excluded.

It has been shown in previous studies (VERZEANO, 1955, 1956; VERZEANO and CALMA, 1954; VERZEANO and NEGISHI, 1960a and b) that the periodic bursts of spikes observed in the nucleus reticularis, in other thalamic nuclei and in the cortex, are related to the spontaneous or evoked circulation of impulses through the neuronal networks of these structures. The differences in the temporal characteristics of the bursts which occur in the two nuclei examined in this study might be related to differences in the pathways that such circulating neuronal activity follows in the two different neuronal networks of these nuclei.

Acknowledgements—It is a pleasure to acknowledge many fruitful discussions on this subject with Professor FREDERICK CRESCITELLI of the Department of Zoology, UCLA.

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FURTHER STUDIES OF PHOTO-CHEMICAL REACTIONS IN LIVING HUMAN EYES

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Abstract—The method of rapid fundus reflectometry was applied to a detailed study of light-sensitive reactions in foveal and, mainly, extra-foveal parts of the human retina. The validity of the Bunsen–Roscoe law was found to be limited. At very high intensities, changes were observed which may be due to transient retinal oedema. Photo-labile material other than rod visual purple was easily detected: comparison with results obtained for the fovea suggests that the cone-pigments, primochrome and secundochrome, are present also in extra-foveal regions. Both bleaching rates and the amount of pigment bleached support the view that the cone inner limb has the ability to change the vergence of the incident light.

Résumé—On a appliqué la méthode de mesure rapide de la réflexion du fond d'oeil à l'étude des reactions photo-sensibles dans la fovéa et la périphérie de la rétine humaine. On a découvert des limitations de la loi de Bunsen–Roscoe, et observé un effet transitoire en employant des brillances élevées, effet dû peut-être à l'oedème rétinien. Des matériaux photo-labiles autres que le pourpre visuel des bâtonnets furent découverts facilement: une comparaison entre les résultats fovéaux et extra-fovéaux suggère que les pigments fovéaux, primochrome et secundochrome, se trouvent aussi dans des régions non-fovéales. La vitesse de blanchissement et la quantité blanchie mènent à l'opinion que le segment interne du cône peut changer la convergence de la lumière.

Zusammenfassung—Die Methode der schnellregistrierenden Fundusreflektometrie wurde bei einer eingehenden Prüfung der Belichtungsreaktionen in fovealen und extrafovealen Teilen der menschlichen Netzhaut verwendet. Die Gültigkeit des Bunsen–Roscoeschen Gesetzes wurde als beschränkt gefunden. Hohe Beleuchtungen führten zu vorübergehenden, ödemähnlichen Veränderungen. Es konnten lichtempfindliche, vom Sehpurpur verschiedene Stoffe nachgewiesen werden: ein Vergleich mit Resultaten, die von der Fovea stammen, besagt, dass die Zapfenpigmente, Primochrome und Secundochrome, auch ausserhalb der Fovea zu finden sind. Die Ausbleichungsgeschwindigkeit und die Menge der ausgebleichten Substanz deuten darauf hin, dass das innere Glied des Zapfen die Lichtvergenz ändern kann.

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ALTHOUGH human colour vision is most highly developed in the retinal fovea, it is by no means restricted to this region. Nonetheless, the reverse is commonly assumed. The erroneous nature of this view has been demonstrated by numerous sensory and electro-retinographic experiments (WEALE, 1956) which show beyond any reasonable doubt that a large part, if not the whole, of the light-adapted human retina can mediate the differentiation of colour.

Vertebrate vision depends on the existence of light-sensitive substances in the retinal receptor outer-limbs (DARTNALL, 1957). Visual purple, a widely distributed photo-labile substance or visual pigment, is easily detected *in vitro* and *in vivo* (WEALE, 1953). It is believed to be contained in rods (but cf. DARTNALL, 1960a, for its presence in a pure-cone retina). Mixtures of pigments were analysed by the method of partial bleaching (DARTNALL,

1950). Applied to the eyes of living guinea-pigs (WEALE, 1955a), this method showed the retina of this animal to contain photo-labile material in addition to visual purple. KOLMER (see MÖLLENDORFF, 1936) states that the proportion of cones in that retina is comparable with that in human extra-foveal regions. If a mixture of pigments can be detected in the eyes of guinea-pigs, it would seem perfectly natural to look for one in man.

At first sight, the experimental evidence is discouraging. We know from histological studies (ØSTERBERG, 1935; FINCHAM, 1936) that the rods greatly outnumber the cones. Extracts from human retinae, whether dark-adapted (CRESCITELLI and DARTNALL, 1953) or not (WALD and BROWN, 1958) have failed to reveal the presence of any photo-labile substance other than visual purple. Measurements performed in a region of the living

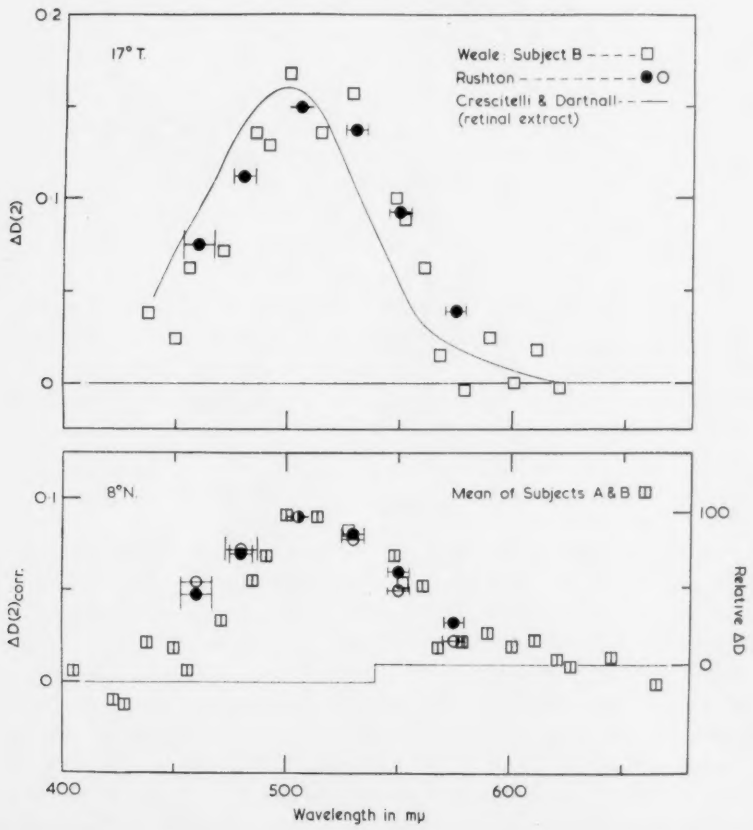

FIG. 1. The spectral variation of changes in the reflectivity of the human fundus (−log retinal transmissivity) at two extra-foveal positions. *Abscissa:* wavelength in mμ; *ordinate:* density change. The black circles represent exposure times of 2 min, the white ones of 10 min, the squares of a half-minute. Note the systematic discrepancy between retinal extract and the living retina (top). The density difference in the bottom diagram (⊡) was obtained by subtracting the density difference obtained with red light (Fig. 8) from that obtained with white light (Fig. 5). The fact that Rushton's zero-line (right-hand scale) is arbitrarily fixed (see p. 370) has been allowed for as indicated by the break. (The number of experiments *N* of which the top diagram (□) represents the mean is 6. In view of the derivation of the lower diagram (⊡) an *N*-value would be meaningless.)

human eye (top, Fig. 1), where the rod–cone ratio is large, tell the same story. These measurements, described in more detail below, represent difference spectra, i.e. measures of changes in the spectral transmission factor of the human retina, when it has been changed from the dark-adapted to the light-adapted state. Both the present and RUSHTON's data (1956a) show this change to be maximal in the green part of the spectrum, approximately at 510 mμ, and both deviate from the difference spectrum obtained by bleaching a solution of a retinal extract (curve, Fig. 1). There is no indication that material other than visual purple and products of its photolysis are involved (DARTNALL, 1960b).

Now RUSHTON (1956a) and DARTNALL (1959) have shown that such a deviation, observed also in receptor suspensions (ARDEN, 1954) and in intact, excised retinae (DENTON and WYLLIE, 1955), can be attributed to incomplete bleaching when a primary product of bleaching is formed and distorts the difference spectrum. Even so, however, there is no indication that material other than visual purple is involved in the derivation of the difference spectra shown in the upper part of Fig. 1.

It must be emphasized, however, that Rushton's difference spectrum and the present one compared with it in this figure were obtained in a retinal region, characterized by a large rod–cone ratio, i.e. one which favours the isolation of visual purple and consequently makes the detection of cone-pigments *a priori* more difficult. But if we probe nearer the fovea, say at 8°, this is no longer true, and more systematic deviations from a visual purple difference spectrum are revealed. Agreement with such a spectrum can be approximated to only when the raw data (Fig. 5) are corrected by subtracting from them the difference spectrum of a red-sensitive component (Fig. 8), a procedure based on the method of partial bleaching (DARTNALL, 1950, 1957). The resultant comparison with Rushton's data obtained for a region much poorer in cones is shown in the lower part of Fig. 1. The agreement is more satisfactory with than without the correction, and it follows that the question of the presence of cone-pigments in extra-foveal regions deserves closer attention than it has received so far.

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TECHNIQUE

The principle of the technique is based on the fact that light entering the eye in general passes through the retina, is partly reflected at the fundus oculi, retraverses the retina, and emerges from the eye in measurable amounts. Less light emerges from the eye if the retina contains light-absorbing material than when this has been bleached away. In practice, a relatively intense beam is used to achieve a change in retinal transmissivity and a weak one to measure it. The method employed in the present study has previously been described (WEALE, 1959), the only alteration concerning the fixation arrangement. The apparatus is shown in plan in Fig. 2a, and part of it in elevation in Fig. 2b.

The source of light was provided by a Xenon arc (type XBO 162) run off d.c. Light from the arc (S_1) (Fig. 2a) was passed through a heat-absorbing filter (C_1) of Chance glass (CN 20) and condensed on to a slit (I) with lens (L_1). The beam was collimated with lens (L_2) and passed through the interference filter (W). The latter was one of twenty-six filters (manufactured by Geraetebau Anstalt of Liechtenstein) and calibrated by the National Physical Laboratory. Their peak transmission was about 20 per cent and they covered amongst them a range from 405 to 680 mμ. Their 50 per cent band-width was approximately 7 mμ. They were mounted in spectral order on a wheel run at 1·2 rev/sec. Every filter was covered with two pieces of polaroid (maximum transmissivity for white light $\approx$20 per cent) in such a way that the two planes of polarization were perpendicular to each other. After passing

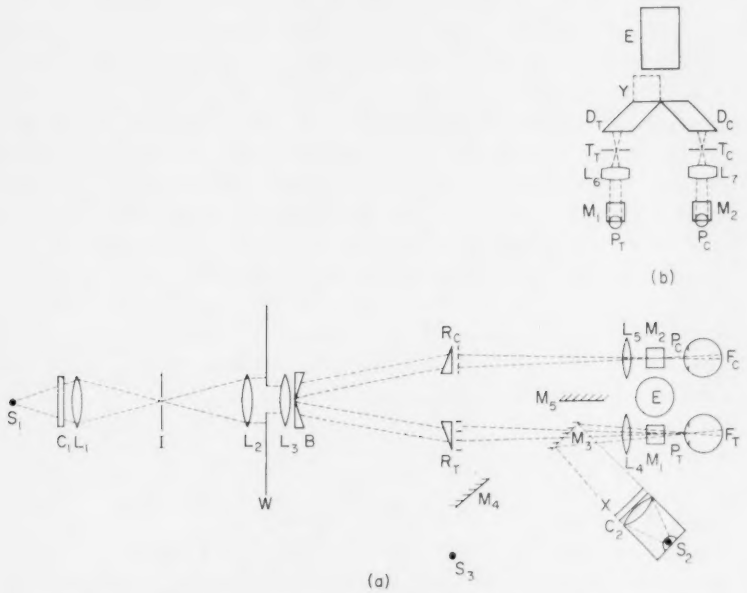

FIG. 2. Apparatus (not to scale): (a) plan of afferent, (b) elevation of efferent optics. (For details see text.)

through lens (L_3) the light beam was split by a bi-prism (B), with "bases out". (L_3) formed images of the slit (I) in the plane of the pupils (P_T) and (P_C) respectively. But before the two beams arrived here, each passed through another prism (R_T) and (R_C), the refractions of which were equal and opposite to those of the two components of the bi-prism (B). Consequently, the two beams entered (P_T) and (P_C) along paths which were parallel to each other. Each of the prisms (R_T) and (R_C) was covered with a piece of polaroid, the planes of polarization of which were perpendicular to each other. This arrangement ensured that light from the arc reached either (P_T) or (P_C), but never both simultaneously. In front of (P_T) and (P_C) there were two spectacle lenses (L_4) and (L_5), which focused an image of one side of the bi-prism (B) on the retina of an approximately emmetropic eye. After reflection at the fundi (F_T) and (F_C) the light emerging from (P_T) and (P_C) respectively was intercepted by the roof prisms (M_1) and (M_2) and reflected upwards. The hypotenuses of these prisms were silvered and covered with shellac. Each of the beams was brought to a focus by achromatic lenses (L_6) and (L_7) (Fig. 2b) so that an image of the retina was formed in the plane of two metal plates (T_T) and (T_C). Each of these was pierced, the aperture coinciding with the image of the retinal image of the bi-prism (B). This arrangement minimized the effect of light scattered by tissues lying in planes not conjugate with that of the retinal image. After traversing the apertures, the two beams were deflected by rhomboid prisms (D_T) and (D_C), so as to be superimposed in space (but interwoven in time) on the cathode of the electron-multiplier (E).

(M_3) was a mirror which could be placed into the light-path of (P_T) so that the bleaching light from the car lamp (12 V 48 W) (S_2) could be directed at the same part of the fundus (F_T) as was illuminated by the test-beam. The filament of this lamp was focused in the plane

of the pupil (P_T), the light having passed through a heat-absorbing filter (C_2). The voltage of the lamp was under manual rheostatic control, and the intensity and spectral distribution of the bleaching beam could be varied by the insertion of neutral density and Ilford Spectrum filters at (X).

Monocular fixation of the right (test) eye was ensured with light from a red luminous spot (S_3) suitably directed by mirror (M_4) when the nasal, and an additional mirror (M_5) when the temporal side of the right retina was studied. In experiments on the fovea use was made of a small black spot painted on the prism (R_T). This was irregular in outline so that the subject could fixate on any convenient excrescence in the outline.

The angular size of retina illuminated by the test-beam was $1{\cdot}4^\circ \times 0{\cdot}75^\circ$; that illuminated by the bleaching beam was circular, $2{\cdot}9^\circ$ in diameter.

The electron-multiplier (E) was coupled to a Cossor oscilloscope. Consequently, whenever its photo-cathode received light either from the test-eye or the control glass-eye F_C, there was a deflection in the (Y)-direction.

SUBJECTS

The subjects tested were "A" and "B" of the previous investigation (WEALE, 1959). During the experimental period, A was in her early twenties, B in his middle thirties. It was not considered necessary to correct the slight refractive errors (FERREE and RAND, 1932). The right eye was homatropinized, and every experiment preceded by total dark-adaptation lasting 20 min for extra-foveal, 12 min for foveal regions.

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EXPERIMENTAL PROTOCOL

Table 1 summarizes the main types of experiment here reported.

TABLE 1.

Retinal position	Reference number	Experiment	Subject	Bleaching light
8°N	1	Effect of light intensity	A, B	White
0°	2	Effect of light intensity	A	White
	3	Pupillometry	A, B	White
	4	Measurement of absolute threshold for white light	A, B	White
	5	Constancy of luminance match	A, B	Violet (Ilford 601) Yellow (Ilford 626)
	6	Test for cone-pigments	A, B	Deep-red (Ilford 206)
	7	Effect of light intensity	A, B	Yellow (Ilford)
	8	Rate of regeneration	A, B	White
	9	Validity of the Bunsen–Roscoe law	A, B	White
10°T	10	Effect of light intensity	A, B	White
	11	The effect of delaying measurements in testing the Bunsen–Roscoe law	B	White
13°T	12	Validity of the Bunsen–Roscoe law	A	White
	13	Effect of light intensity	A	White
17°T	14	Effect of light intensity	A, B	White

The retinal illuminations used are shown in the Figures.

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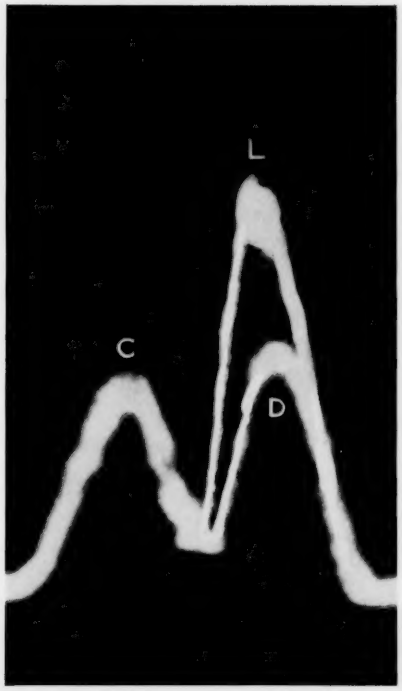
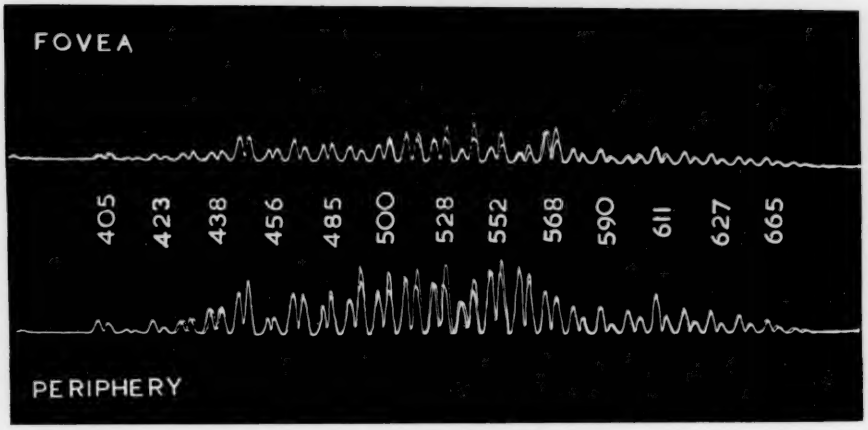


(*a*)



(*b*)

FIG. 3a. Trace due to artificial control C. Trace due to the dark-adapted (D) and light-adapted (L) eye respectively obtained with light of $\lambda = 552$ mμ. The density change $\Delta D(2)$ is computed in terms of the heights of these traces. The two traces due to the artificial eye, and recorded when (L) and (D) were recorded, superpose accurately and hence appear as one.

b. An extension of the above to cover the whole of the spectrum with wavebands centred at wavelengths shown in between the two sets of records. Note that the maximum density change in the fovea occurs at a wavelength much longer (561) than is true of the extra-fovea (528).

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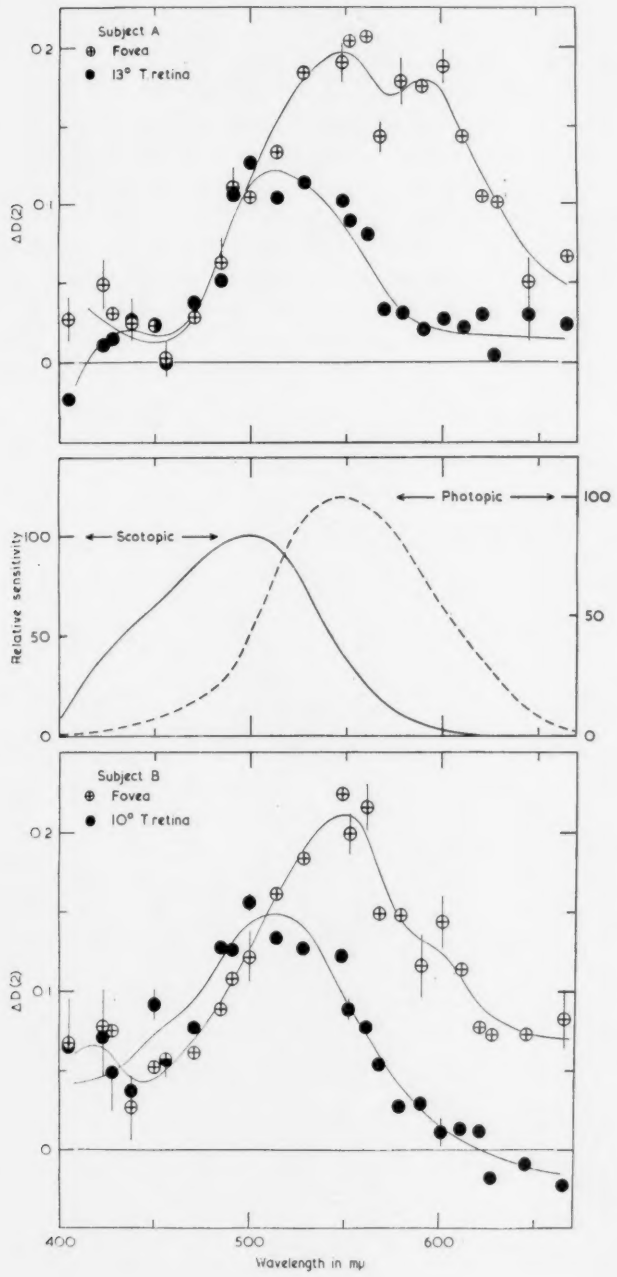

FIG. 4. Foveal and extra-foveal density-difference spectra for two observers compared with the photopic and scotopic spectral sensitivity curves of the standard eye (centre).

⊕: $N_A=32$, $N_B=19$; ●: $N_A=15$, $N_B=16$.

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As described in the previous paper (WEALE, 1959), the basic measurements involve the comparison of the photographic records of the oscilloscope traces. These responses are due to the incidence on the multiplier (E) of light emanating alternately from the artificial and the test-eye respectively. The top of Fig. 3a shows the superposition of two responses obtained with light of mean wavelength=552 mμ before (D) and after (L) exposing the dark-adapted fovea to an intense white light. The left-hand portion of the trace (C) shows that the apparatus remained constant, for the two traces from the artificial eye are seen to coincide. But the response from the test-eye is much greater after than before bleaching, photolysis having removed light-absorbing material. Fig. 3b shows a similar superposition for the complete spectrum: the top trace refers to the fovea, the bottom to the periphery (8° nasal). It is easily seen that, in the former, the principal change occurs in the yellow–green part of the spectrum ($\approx$560 mμ), while in the latter case it is situated in the green ($\approx$510 mμ). This is shown graphically in Fig. 4 where typical results obtained with intense white bleaching lights for the fovea and 8° nasal retina are compared. The obvious correla-

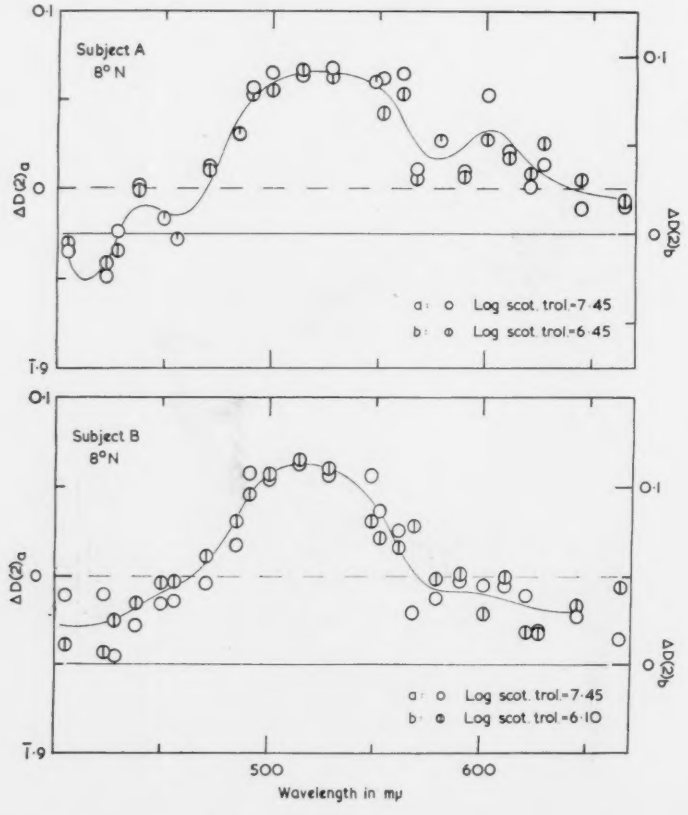

FIG. 5. Density-difference spectra for white light. Note that the broken line represents the base-line for scale (a) on the left which belongs to the data (O); the continuous line represents the base-line for scale (b) on the right which belongs to the data (⊕).

O: N_A=21, N_B=29; ⊕: N_A=18, N_B=21.

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tion with the photopic and scotopic spectral sensitivity curves (CIE mean V_λ curves) suggests that these differences provide a basis for the Purkinje shift.

The results were computed as previously described (WEALE, 1959), the number of experiments (N) being indicated in the legends to the figures. The ordinates $\Delta D(2)$ refer to the measured density change for double transit through the retina, and represent the lower limit of twice the actual change if all the rays retrace their path, and of the actual change if none of them does (WEALE, 1957).

Although a handful of repeats was adequate to give a broad outline of a given difference spectrum (top, Fig. 1), more numerous repetitions were made, e.g. when a series yielding an unexpected result was to be checked, or when it acted as a control for another type of experiment.

The choice of extra-foveal positions studied was dictated by physiological and technical considerations, and they cover eccentricities much studied by other workers (MORELAND and CRUZ, 1959; WEALE, 1956).

The stimulus values are expressed in scotopic trolands. Reference to the work of SPRING and STILES (1948) shows that no serious error arises from the neglect of the variation of the effective pupil area with eccentricity over the angular range examined. It has recently been suggested that the troland, as defined at present, can lead to erroneous results (RICHTER, 1956; WEALE, 1961a). The data in the figures, however, embody the usual definition.

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RESULTS

Changes due to White Light: 8° Nasal

Data obtained with the two strongest bleaching lights employed are shown in Fig. 5. The wavelength scale is plotted along the abscissa as usual. But the ordinate scale on the left refers to the highest bleaching intensity, that on the right to one lower by a factor of 10 for subject A, and a factor of 22 for subject B. The reason for this is as follows. It was noted that the density changes measured for the highest bleaching intensity were systematically lower than those obtained with either of the weaker lights. Closer examination revealed that the data obtained for the two levels were substantially similar in all respects except that the base-line of the top-intensity measurements had dropped. The drop amounted to some 0·025 logarithmic (i.e. density) units for subject A, and 0·05 such units for subject B. It was largely independent of the wavelength of the measuring light, a factor clearly revealed by the method of plotting the data in Fig. 5.

Substantially similar data, i.e. maximal at 520–530 mμ, were obtained at lower bleaching intensities, but no change in zero-line was observed.

Changes due to White Light: the Fovea

The above finding necessitated a brief re-examination of the fovea. Subject A's central region was bleached with white lights of top intensity and one tenth of this, the experimental runs being interlaced. A similar shift in base-line was observed.

Pupillometry

A reduction in diameter of only 3 per cent during bleaching could conceivably account for the drop in the zero-line. To examine this point the mydriaticized pupil was photo-

graphed under the conditions of the experiments. Experiments at the two top intensities were also done with a stop in a plane conjugate with the pupil and located in the emerging beam so that light passing only through the central part of the pupil was allowed to fall on the photo-multiplier. Both experiments showed that pupil changes were not responsible.

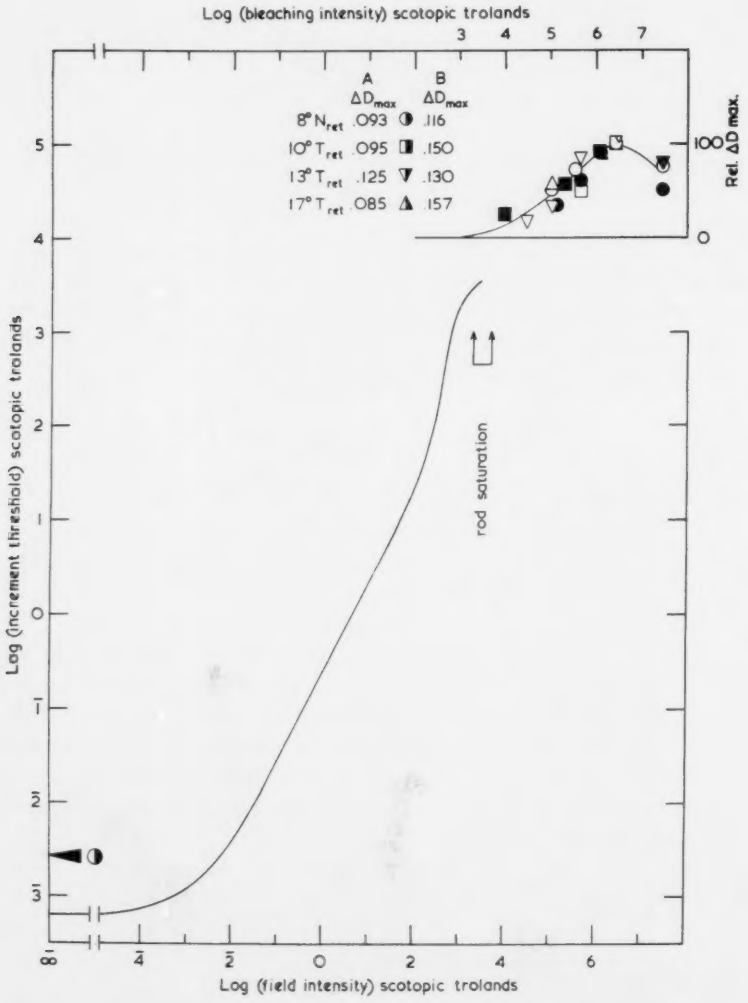

FIG. 6. *Bottom:* AGUILAR and STILES' (1954) mean curve relating the rod incremental threshold (ordinate) to the intensity of the adapting field (abscissa). The mean threshold of subjects A and B (present paper) measured for zero background is indicated with the arrow on the left. *Top:* The relative maximum density change (ordinate on right) as a function of the (white) bleaching intensity which corresponds to the adapting intensity of the curve of Aguilar and Stiles. The points obtained for subjects A and B at various retinal positions are shown against the actual measured maximum density changes. Note that the rods are "saturated", i.e. the incremental threshold approaches infinity before bleaching takes place, as predicted by Aguilar and Stiles.

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Measurement of the Absolute Threshold

In order to relate the bleaching intensities to visual function, it was desirable to express them in terms of the absolute visual threshold. This was defined as that intensity which gave rise to a 50 per cent chance of seeing the stimulus presented for 0·036 sec and subtending at the eye an angle of 1·7°. The stimulus was provided by the same source as used for bleaching (WEALE, 1959). It was nominally white: the neutral density filters used were calibrated for white light only. Dark-adaptation preceding the measurement lasted 30 min. Measurements were restricted to a nasal retinal region at 8°. The values for the two observers A and B were 3·73 and 3·16 log scotopic trolands respectively. The average of the two is shown in the left-hand bottom corner of Fig. 6.

Luminance Matching

If the light-sensitive material present in extra-foveal regions is homogenous then two different spectral stimuli equally luminous at a low-luminance level can reasonably be

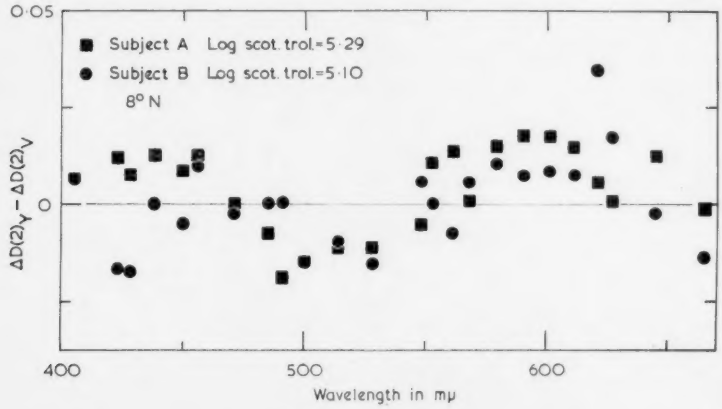

FIG. 7. The difference between the difference spectra obtained with yellow and violet bleaching lights of equal scotopic luminance.
Y: $N_A=17$, $N_B=20$; *V*: $N_A=16$, $N_B=34$.

expected to give rise to similar density changes. But stimuli matched under scotopic conditions produce bleaching which is too small to measure as is readily seen from the top part of Fig. 6. In this figure there is shown the maximum density change produced by white lights of stated intensities, retinal position forming a parameter. The scotopic region extending to 2 or 3 log units above threshold, such intensities are clearly too low. However, the above principle should hold if both stimuli are multiplied by equal factors. Then, if the prediction is valid, the difference between the two density changes, one produced by each light, should be zero throughout the spectrum.

In order to test the prediction a yellow (Ilford 626) and a violet (Ilford 601) filter were placed in the path of the white bleaching beam. They were juxtaposed in a plane conjugate with the retina and neutral density filters added to one side or the other, till they matched at a level of log scotopic trolands $\approx 1{\cdot}5$. Preceding dark-adaptation having lasted for 30 min, the colour difference had disappeared (WALD, 1960). (A red bleaching light (Ilford 206) was

matched under similar conditions against white, but here the discoloration was much less pronounced.) As before, measurements were made only at 8° in the nasal part of the retina. The bleaching experiments were done with intensities which were a fixed multiple of the yellow and violet matching intensities, determined in the luminance match. The neutral density filters were not tested for neutrality. Let us assume then that, although a good match had been made, removal of the filters to produce a measurable density change favours light of short wavelengths. This means that the violet light is stronger than the yellow and the difference between the two difference spectra will simply be another difference spectrum corresponding to that of the allegedly simple pigment involved. The same applies if the yellow light is stronger except that the sign of the difference spectrum is reversed. Fig. 7 shows neither of these expectations to be fulfilled. Except for the blue part of the spectrum the agreement between subjects A and B is remarkably close. The data suggest that the yellow stimulus bleached material preferentially in the long-wavelength part of the spectrum while the violet bleaching light was more effective at shorter wavelengths although the two lights were visually equivalent under scotopic conditions.

Changes due to Red Light

Neither the difference spectra shown in Fig. 5 nor the results quoted in the previous section are consistent with the view that only visual purple is being bleached. But they do not

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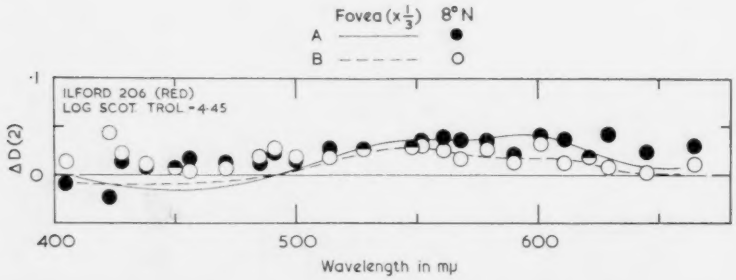

FIG. 8. Difference spectra obtained with a deep red bleaching light in foveal (curves), and extra-foveal regions (circles) respectively.
$N_A = 14$, $N_B = 18$.

tell us what causes such discrepancies as are revealed. Deep red light which is without much effect on visual purple can help here and accordingly it was used in a study of the nasal retina at 8°. This was a particularly interesting experiment to do because the same bleaching light had been used on the same observers in a study of the fovea (WEALE, 1959). The results are shown in Fig. 8. Those obtained for the foveae are shown by the curves, but those for the 8°N position by the symbols. The former have been scaled down by a factor of 3 to facilitate the comparison between the respective spectral variations. The agreement is good for the middle of the spectrum towards longer wavelengths: even the inter-observer difference revealed in the foveal data (and confirmed there with white bleaches) is repeated extra-foveally. It is possible that some visual purple is being bleached, after all, for reference to Fig. 6 shows that white light of the same scotopic luminance would have produced a similar density change at 515 mμ. On balance, these data suggest that one or more pigments

other than visual purple are present at 8° N, for if the spectra in Fig. 8 are subtracted from those in Fig. 5, the data in the lower part of Fig. 1 are obtained. And these, as we have seen, are in tolerable agreement with the visual purple density difference spectrum. The fact that a period of dark-adaptation of only 3 min causes a smaller but still measurable and similar density difference spectrum to be obtained lends support to the view that we are, in fact, dealing with long-wavelength sensitive material, which may well be primochrome and secundochrome (WEALE, 1961b). (These terms, representing green-sensitive (WEALE, 1955b, 1958a) and orange-sensitive (RUSHTON, 1958) material found in pure-cone retinae, are preferable to other specific names. Until these presumptive pigments are extracted and identified, taxonomy seems premature, and a system of nomenclature reflecting the order in which the bleaching effects were discovered—similar to the one used in classifying colour-defects—less confusing.)

Changes due to Yellow Light

As visual purple is sensitive to yellow light, one might reasonably expect some kind of intermediate result when the retina at 8° N is exposed to it. More energy being available in this spectral range, it is feasible to study photo-chemical changes as a function of bleaching intensity.

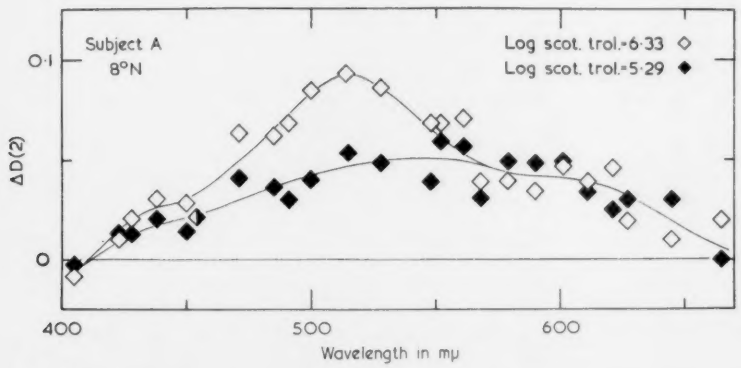

FIG. 9. Difference spectra obtained with yellow lights of two different intensities. $N\diamond = 13$, $N\blacklozenge = 17$.

The results are shown in Fig. 9 for subject A, those for subject B being similar in all major respects. In the first place, the low intensity results obtained with an exposure only four times as strong as those described in the previous paragraph, differ from them largely only in the enhanced density change recorded for shorter wavelengths. It is as though the exposure used in the red-light bleaches were saturating and no more could be bleached even though the bleaching intensity is increased (cf. white-light bleaches done in this retinal region of 8° shown in Fig. 5). Secondly, an increase in the intensity of the yellow bleaching light by a factor of ten, increases the recorded density change at 515 to a figure comparable with that obtained with a white-light bleach of similar scotopic luminance (Fig. 6). The photo-chemical nature of the hump at about 600 mμ is also illustrated by the finding that it can be avoided only by using a violet bleaching light. These observations, then, support

the belief in the existence of photo-sensitive material additional to that causing the maximum change at 515–20 mμ, largely attributable to rod visual purple.

The Rate of Regeneration

This was measured in the same manner as previously described for the fovea (WEALE, 1959) by varying the period of dark-adaptation after exposing the eye to an intense light. Then a record was taken of the dark-adapted fundus, the eye bleached, and another record taken. Clearly the longer the eye was left in the dark after the first exposure, the more material would be able to be bleached on regeneration. Fig. 10 shows these expectations to be fulfilled: regeneration at 8° is initially approximately three times as slow as in the fovea. Visual purple is believed to regenerate more slowly still (RUSHTON, 1959): this suggests that regeneration of cone-pigment as well as of visual purple is observed at 8°N.

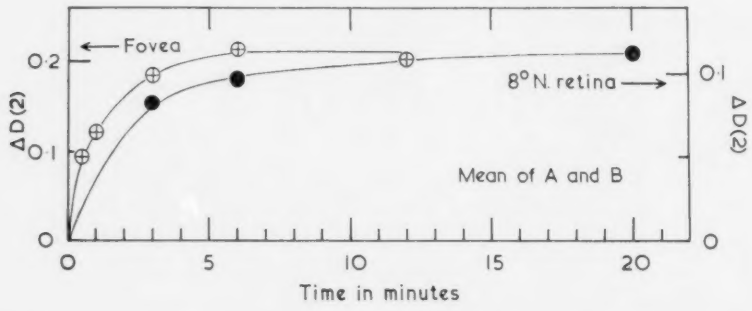

FIG. 10. Comparison between the regeneration of bleached pigment in foveal and extra-foveal regions respectively, the averaged measurements for subjects A and B referring to the maximum change.

The Validity of the Bunsen–Roscoe Law

According to this law, the magnitude of a photo-chemical change depends on the product ($I \times t$), intensity × time. Its validity implies that interaction between matter and radiation is taking place, but it does not necessarily imply that such interaction affects only one substance. Nor does the failure of the Bunsen–Roscoe law necessarily imply that the change under consideration is non-chemical in nature, i.e. the failure may be only apparent. Products of the change may behave differently when I is large and t short than when the reverse holds.

In the present study the law was tested by using exposures of 5 and 30 sec respectively. In the former case, the luminance was approximately 6·3 log scotopic trolands; in the latter 5·5. Subject A was examined at an eccentricity of 10° and 13° temp. Subject B only at 10°, but an important additional experiment was performed in this instance. Whereas the record of the reflexion spectrum for the bleached eye was obtained at the expiration of the 5 sec exposure for both A and B, further measurements were made on B, the bleaching light having been switched off after 5 sec but the recording being made after the lapse of another 25 sec.

The measurements at 13° showed that the Bunsen–Roscoe law was approximately obeyed, i.e. the density spectra for the long weak and short intense exposures respectively

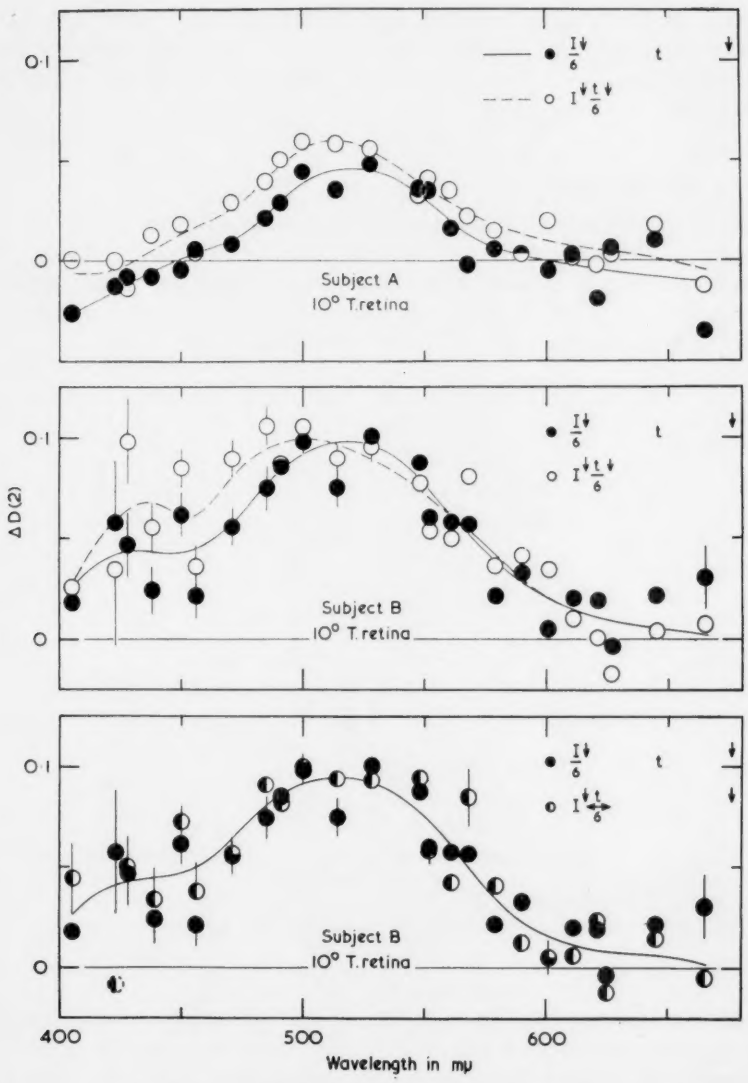

FIG. 11. Tests of the validity of the Bunsen–Roscoe law. (For details see text.) The vertical arrows in the three insets indicate the time of recording the traces. Thus in all three cases the reflectivity of the dark-adapted fundus was measured just prior to the onset of the bleaching exposure (t) lasting 5 or 30 sec. The second and final record was taken immediately after cessation of the bleaching period in the experiments shown at the top and centre, but 25 sec later in the (t/6) experiment shown at the bottom.

Top: $N_{\circ}=9$, $N_{\bullet}=8$; *Centre:* $N_{\circ}=18$, $N_{\bullet}=18$; *Bottom:* $N_{\circ}=19$, $N_{\bullet}=18$.

were similar. At 10°, however, both A and B showed a breakdown of the law (Fig. 11). In both cases there is a spectral shift, the maximum change for the short intense exposure occurring at a wavelength 10–20 mμ shorter than that corresponding to the long weak exposure. In addition, subject A showed a small quantitative discrepancy, the short intense

exposure giving rise to a somewhat smaller density change than did the long weak exposure. The additional experiment for subject B showed that, if recording is delayed for 25 sec, validity of the Bunsen–Roscoe law will be observed under conditions which reveal its failure when recording is immediate.

Variation with Retinal Position

Although the measurement of maximum density change as a function of retinal eccentricity was not one of the prime objects of this study, it did yield data of interest. These are shown as an inset to Fig. 6. While the number of retinal locations studied is small, subject A shows a maximum at about 12° in the temporal side of the retina, while subject B shows a plateau, essentially and significantly different from A's data.

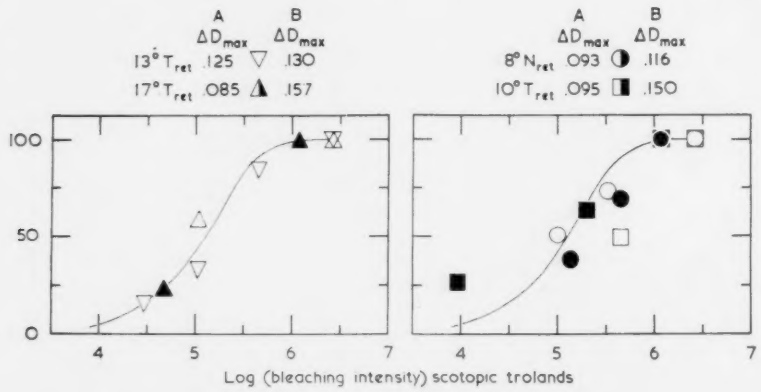

FIG. 12. The relative maximum density changes as a function of the intensity of white bleaching light for regions remote (left) and nearer (right) the fovea respectively. This figure represents an analysis of the data shown in Fig. 6. The curve is theoretical and one of the assumptions which it is based on is that regeneration is negligible during the time of bleaching.

This figure also shows the maximum density changes recorded for the wavelength range of 510–520 mμ with white bleaching lights of various intensities. The curve is drawn freehand and suggests that, when the exposure lasts 30 sec, measurable bleaching is unlikely to occur with retinal illumination of less than 3000 scotopic trolands. Now it follows from elementary bleaching kinetics (DARTNALL, 1957) that, if density and maximum density difference due to bleaching are approximately equal, the density should be related to the exposure ($I \times t$) by an exponential relation. In itself such a relation provides no means for testing whether one is dealing with one or more photo-labile substances: for if there are two different substances with the same photo-sensitivity and they fulfil certain well-established conditions (DARTNALL, 1957), this relation will still be obeyed. It is represented in Fig. 12 by the curve. The data obtained at distances more remote from the fovea follow the expected course (Fig. 12a) more nearly than do those nearer to the retinal centre (Fig. 12b). The cause for the discrepancy in the latter is unknown, but could be explained in terms of rapid regeneration.

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DISCUSSION

The Accuracy of the Data

There is no denying that though under the best conditions an accuracy of some 5 per cent can be achieved, the scatter in the data is sometimes large. This is particularly true at the short-wavelength end of the spectrum (Fig. 11). However, averaging the relatively large number of points gives repeatable results (Figs. 1, 5). The cause of the scatter is partly attributable to the small signal–noise ratio at some of the wavelengths employed. But nothing can be done at present short of robbing the technique of the advantage of rapid recording. A fuzzy photograph of how the horse managed to bolt is preferable to a distinct picture of the locked but empty stable.

The White Bleaches

There is little doubt but that the major portion of the density changes produced with white light is attributable to the photolysis of visual purple. The evidence for this view is as follows. The type of difference spectrum obtained in a study of extra-foveal regions differs from that found in experiments on the fovea (Fig. 4). Hence, as the phenomenon observed—namely a change in fundus reflectivity—is attributable to irradiation of the fundus, the properties of the fundus or of parts overlying it must alter. A change in macular pigment, which by its high concentration in the fovea (STILES, 1953) offers one such possible difference, can be ruled out for it does not absorb in the green part of the spectrum (510–520 mμ) where the changes are observed to be maximal. However, photo-chemical studies of the intact rod cell (e.g. ARDEN, 1954; DENTON and WYLLIE, 1955) have shown that when visual purple is bleached it produces a density difference spectrum similar to that obtained by white bleaches of the living human eye. We have seen that such discrepancies as are revealed are probably due to the presence of cones. The view that the changes in fundus reflectivity represent the bleaching of photo-sensitive material is reinforced by the data as plotted in Fig. 12, where the curve represents the relation

$$D_E = D_M e^{-cE}$$

D_M being the maximum density change which can be achieved and measured, D_E the change due to an exposure smaller than the least exposure giving rise to D_M, and c is a constant. E is equal to $I \times t$ where I is the energy flux per unit time and t the exposure time. For retinal positions of 13° and 17° the experimental points agree with the theoretical relation.

A further argument in favour of the view that visual purple is being bleached is connected with the measurements of the absolute threshold. PIRENNE (1956) has suggested that the rate of bleaching and the absolute threshold should be related quantitatively, and it may be shown that the fraction p of pigment bleached is related to the number of quanta Q absorbed at the absolute threshold by the relation:

$$Q = \frac{p\alpha t A N v}{T R \gamma D}$$

where the meaning of the symbols is as follows:

α = the effective percentage absorption of the visual pigment (PIRENNE, 1956);
t = time of exposure of threshold test stimulus;
A = area of threshold test stimulus;

N = number of rods per square degree;
v = photosensitivity;
T = bleaching time;
R = ratio of bleaching ÷ threshold intensity;
γ = quantum efficiency;
D = molecular orientation effect (DENTON, 1954).

The assumptions underlying this expression have previously been discussed (WEALE, 1961c). The fact that $Q=7$–14 as found on substituting the stated values (allowing for some uncertainty in them) agrees well with accepted values for this quantity (PIRENNE, 1956), and supports the view that visual purple is being bleached.

The apparent reduction in density for the highest intensity employed is unexpected (Figs. 5, 6) and has been shown to be due to a change in the base-line. A similar change in base-line could not be detected at lower intensities. Photographic pupillometry (which could have registered a change in pupillary diameter three times smaller than that required to explain the change in base-line) and the experiments with the pupil stop exclude the possibility of ascribing the effect to pupillary changes.

A similar effect, possibly due to retinal oedema, has previously been observed in the decerebrate, curarized cat (WEALE, 1953) where pupillary constriction can be ruled out. Local heating was thought to be unlikely. The phenomenon cannot be attributed to migration of the epithelial pigment granules for the tapetal region lacks these: but changes in the position of the receptors cannot be ruled out. Experiments on the Stiles–Crawford effect at luminance levels revealing the oedema phenomenon might help to clarify the situation.

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The Fovea

The "oedema" effect occurs also in foveal bleaching, a fact unknown when the data on the fovea were published (WEALE, 1959). This has several consequences for the interpretation of those results. In the first place the maximum density difference for white light (Fig. 4) is appreciably larger than was then thought (namely 0·16 approx.). It is, in fact, of the order of 0·2; as it is unlikely that the light retraces its path in cones (WEALE, 1957) this $\Delta D(2)$ value probably approaches the value for single transit. Geometrical consideration might easily harmonize this with BRINDLEY's estimate (1953) of 0·9. Secondly, regeneration occurs faster than was then believed, a factor which tends somewhat to increase the discrepancy between these data and those of RUSHTON (1958). Thirdly, the fading of the "oedema" effect, which experiments in the present series indicate to be complete within not more than 3 min after cessation of the most intense bleaching exposure, accounts well for the irregularity in the spectral variation of the initial rate of regeneration previously reported (Fig. 7, WEALE, 1959). As the "oedema" effect is only observed with intense bleaching lights, the previous conclusions drawn from foveal bleaching with red light are unaltered. The cause of the discrepancies between the maximum foveal density changes and rates of regeneration as measured by RUSHTON (1958) and the present method respectively is unknown. However, we saw in connection with Fig. 1 that Rushton's method involves the arbitrary fixing of the zero-line. In his foveal work he believed that no measurable density changes occurred at wavelengths longer than 700 mμ. The above discrepancies may be reduced if this assumption is invalid.

The Violet End of the Spectrum

Both the foveal (Fig. 4) and many of the extra-foveal data (Figs. 4, 5, 9, 11) show, superimposed on the scatter, a "hump" in the region of 420–440 mμ. Bleaching was done with violet light in order to ascertain whether this part of the difference spectrum could be affected selectively: however, it was not possible to be sure that a blue–violet sensitive pigment (tertiochrome) was being bleached preferentially. Nor could a less likely but feasible alterative be tested—namely whether the apparent hump is due to the formation of one or more products of bleaching absorbing maximally in the region of 460–470 mμ. The only points worth noting are that subject A, whose retina seemed to contain more secundochrome than that of subject B, gave rise to more marked violet "humps" than did B, and also that there was a tendency for these humps to be less pronounced at greater eccentricity.

Variation with Retinal Position

Although bleaching was studied only in a small number of retinal positions, the results obtained suffice to reveal a significant difference between the two subjects as regards the position of maximum density change (inset, Fig. 6). This is hardly surprising when we bear in mind that measurements of the absolute threshold (of the fully dark-adapted eye) as a function of retinal eccentricity differ from person to person (STILES and CRAWFORD, 1937; CABELLO and STILES, 1950). The similarity between this function and ØSTERBERG's (1935) receptor count done on a single human retina can therefore be only approximate and discourages any serious attempt at even a qualitative comparison of Østerberg's with the present data. It is noteworthy, however, that subject A shows a peak pigment change at about 12°T, the values being less at the other eccentricities, while B has either two maxima or a broadish plateau; some of the above threshold measurements reveal similar variations. These cannot be accounted for in terms of absorption by macular pigment which does not appreciably absorb at wavelengths longer than 500 mμ. This shows that any attempt to base an estimate of the maximum density change and, by implication, of the *in situ* density of all human rods on measurements done in but one retinal position are doomed to failure. For imagine that such measurements are done, say, at an eccentricity of 17° where Østerberg showed rods to be most numerous in the one retina he studied. If we believe that the absolute threshold depends on the number of absorbing chromophores (cf. p. 363 above), and the threshold at 8° is half of its value at 17° (STILES and CRAWFORD, 1937; CABELLO and STILES, 1950), then clearly our claim to have measured the maximum density for all the retina will be open to an unanswerable challenge. We shall, in fact, have measured only about one-half the maximum density with consequences to be examined below.

The Validity of the Bunsen–Roscoe Law

At a retinal eccentricity of 13° CAMPBELL and RUSHTON's (1955) finding that the law was obeyed was confirmed. Fig. 11, however, shows that, in the range measured, the Bunsen–Roscoe law is not valid at 10°, i.e. the density difference is not constant when the product $I \times t$ (intensity I, exposure time t) is kept constant, and t does not exceed 30 sec. Campbell and Rushton, who tested the validity of this law with Rushton's technique on one subject, found the law to be obeyed "fairly exactly for times up to 48 sec." It will be recalled that this technique depends essentially on the measurement of density differences between the blue–green and orange part of the spectrum. Now inspection of the top and middle part of Fig. 11 shows that if one restricts one's attention to these two spectral regions—as is done

in Rushton's method—then there is no differential effect as between the long, weak, and the short, strong exposures respectively. Observer A shows approximately equal, small differences, and observer B zero difference. To this extent, there is complete agreement as between Campbell and Rushton's results on the one hand and the present data on the other. But what Rushton's method fails to reveal is the alteration in the spectral distribution of the density change: the present method—which examines most of the visible spectrum, instead of only two wavelength bands—shows that a reduction in exposure time leads to a shift of the density difference spectrum to shorter wavelengths. There is also the suggestion that long exposures lead to a deficit, an observation made by Campbell and Rushton for exposure times of 90 sec.

One can only speculate regarding the cause of this shift. Work on the cat (WEALE, 1957) showed that a secondary product resulting from bleaching is, in all probability, light-sensitive. More recently, BRIDGES (1960) showed with reference to mammalian visual purple (i.e. rhesus monkey) that the orange photo-product (λ_{max}=480 mμ, cf. WEALE, 1957) bleaches on exposure to light to indicator yellow. The tentative interpretation put on the present results is that such bleaching does, in fact, occur under conditions of intense, short exposures. At long weak exposures there is either marked regeneration or the bleaching of the photo-product does not occur because of the lower quantum efficiency of the process (KROPF and HUBBARD, 1958). The evidence (bottom, Fig. 11) is biased in favour of the former alternative. For the short intense exposure appears to give rise to the same result as the long weak one—i.e. the Bunsen–Roscoe law appears to be valid—if the examination of the retina is delayed for 25 sec.

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It would seem that Campbell and Rushton's belief in the general validity of the law may be due to one or all of the following causes: (1) Rushton's method is unsuitable for the detection of small spectral changes (see below); (2) his measurements take too long (WEALE, 1953); (3) Campbell and Rushton's measurements were restricted to one retinal position (presumably at 15° off centre).

The discrepancy regarding the validity of the law as between retinal positions of 10° and 13° is a little puzzling. However, we noticed a parallel discrepancy in Fig. 12 where maximum density bleaches remote from the foveal centre obeyed the theoretical relation more closely than those nearer the macula. It may be suggested tentatively that complications due to incomplete regeneration could account for both observed discrepancies. Whether this is to be associated with a regional variation in the rate of regeneration of visual purple or to the intervention of cone-pigment regeneration or to some other cause is a point yet to be clinched.

The Chromatic Bleaches

We have noted that even white bleaches suggest that one or more substances other than visual purple were being bleached in the present experiments (Fig. 5).

The results shown in Figs. 7, 8, 9 strongly confirm this view. The luminance matches which form the basis of the comparison between the effects of yellow and blue–violet bleaching lights (Fig. 7) would not be expected to reveal the full amount of material other than visual purple present. This experiment merely provides negative evidence: visual purple is not the only material present. Now Campbell and Rushton failed to find a breakdown of their luminance matches. However, the bandwidth of the filters used in their measurement of the density differences would be expected to reduce the discrepancy

illustrated in Fig. 7 to such small dimensions as to make it indistinguishable from their experimental error. This supports an opinion tentatively advanced in the discussion on the validity of the Bunsen–Roscoe law, namely that Rushton's method appears to be of limited use for the detection of small spectral changes.

The red bleaches (Fig. 8) and the tremendous change in the difference spectrum as the yellow bleaching light is raised in intensity (Fig. 9) support the view that material additional to visual purple is present in this retinal region. A comparison between red bleaching data obtained under similar conditions in the foveae of A and B suggests that the pigments primochrome and secundochrome (WEALE, 1961b) are being detected also outside the fovea. At first sight, it seems surprising that these pigments should be bleached virtually to completion with a yellow light bleaching only half the visual purple present. However, this light is approximately four times as efficacious for the subsidiary pigments as for visual purple. If the rate of regeneration is assumed to be small as compared with that of bleaching then the "chrome" pigments would appear to be at least four times as photo-sensitive as visual purple. If they regenerate faster than visual purple, this ratio is increased, and more so if we recall that, at an eccentricity of 8°, the rod–cone density is high (≈ 11). We have to try and decide, however, which part of the cone provides the effective cross-sectional area, gathering light. If it is the outer limb then this area will be very small as compared with that of eleven rods. But let us consider the inner limbs. In many species (WALLS, 1942) they appear to contain refractile material, which might serve as a lens, gathering and converging the incident light on the light-sensitive outer limb. The ratio of the cross-sections of single rod and extra-foveal cone inner limbs is about 1 : 11. If the ratio of rod and cone numbers at 8° is about 10 : 1 (ØSTERBERG, 1935; POLYAK, 1941) then the *minimum* ratio of the extra-foveal "chrome" to visual purple photo-sensitivities is about 3·6. RUSHTON (1958) obtained twice this value (7) when comparing rods with *foveal* cones.

The possible importance of the light-gathering power of the outer limbs is revealed also in a consideration of the amount of peripheral "chrome" pigments bleached. RUSHTON (1956a) invoked this concept in order to account for a small discrepancy between his result for the visual purple photo-sensitivity in the living human eye and that of DARTNALL, GOODEVE and LYTHGOE (1938) for a solution of a frog retinal extract. The discrepancy amounted to some 70 per cent. Rushton suggested the light-gathering hypothesis to account for this discrepancy. The latter can be shown to be much smaller than he surmised. In the first place, he used a value of 16 mm for the posterior nodal distance of the human eye, the accepted value being 16·7 mm (LE GRAND, 1957). Secondly, Rushton made no allowance for the "black-out index" (LAWSON, 1948): it can be shown that we spend about 10 per cent of our waking time with our eyes shut owing to blinking. Since Rushton does not mention giving any instructions to the contrary it can be assumed that his subjects blinked, and, in view of the demanding conditions, at least at the normal rate. Thirdly—a point unknown when Rushton published his work—mammalian photo-sensitivity appears to be about 10–15 per cent higher than that of frog visual purple (BRIDGES, 1959). These factors reduce the discrepancy between Rushton's experimental and expected value from 70 to not more than 25 per cent. Since Dartnall *et al.*'s measurements of their flux had an accuracy of ± 20 per cent one can confidently say that such a discrepancy as Rushton may wish to account for is negligible—it hardly merits postulating a hypothesis of light-gathering properties on the part of the rods.

But the situation is wholly different when we consider peripheral cones. Fig. 8 shows that the density change produced by red light is about one-third of the change measured for

the fovea. This is very large when we recall the following histological findings. According to POLYAK (1941) the outer limbs of the foveal cones are about six times longer than those of extra-foveal cones. But even in the rod-free region their length drops to about one-half the maximum value. If the outer limbs are really filled with light-sensitive material as they appear to be in the case of rods, then the available light-path in peripheral cones is about six times less than in foveal ones. If, moreover, the pigment concentrations in the two types of cone are of the same order, then the density difference should be in the same proportions, cone for cone. However, the number of cones per unit area at 8° is about one-eighteenth of what it is in the fovea. Hence the density change due to bleaching should be virtually undetectable.

Let us make the following assumptions:

1. The concentrations of pigment in the foveal and extra-foveal cones are equal.
2. The ratio of the optical path lengths in foveal and peripheral cones respectively is (m).
3. The ratio of the effective cross-section is (f). This is to say, if the foveal cones offer no spaces through which light can pass without being absorbed, the effective cross-section being unity, the corresponding value in the periphery is (f). It follows that the fraction ($1-f$) is occupied by rods and inter-receptor spaces: to a first approximation it may be assumed that the part of the incident light-flux covering the area ($1-f$) is reflected at the fundus, and emerges from the eye in amounts independent of whether or not any bleaching with red light has occurred. Then if the change in transmissivity (=negative antilog. of measured density change $\Delta D(2)$) is τ^2_F at the fovea and τ^2_p in the periphery (at 8° N), and the transmissivity of the bleached material is T^2_L, it can be shown that

$$f = \frac{1-\tau^2_p}{1-\tau^2_p\,(1-T^2_L)-T^2_L\,\sqrt[m]{\tau^2_F}} \tag{2}$$

and

$$m = \frac{\log \tau^2_F}{\log\,[1-\tau^2_p\,(1-T^2_L)-(1-\tau^2_p)/f]-\log T^2_L} \tag{3}$$

(T^2_L) is unknown but if we make the reasonable assumption that it approaches unity then (2) simplifies to

$$f = \frac{1-\tau^2_p}{1-\sqrt[m]{\tau^2_F}} \tag{4}$$

and (3) to

$$m = \frac{\log \tau^2_F}{\log\,[1-(1-\tau^2_p)/f]} \approx -f\frac{\log \tau^2_F}{1-\tau^2_p} = f\frac{\Delta D(2)_F}{1-\tau^2_p} \tag{5}$$

Fig. 13 shows plots of function (2) and (3). In the upper part T_L is assumed to be equal to unity and (f) is plotted as a function of (m) (the ratio $\frac{\text{length of foveal cone outer limb}}{\text{length of peripheral outer limb}}$). In the lower part ($m$) is set equal to unity and (f) plotted as a function of (T_L). It follows from these graphs that the calculated value of (f) is at least four times as large as would be expected from a consideration of the relative numbers of cone outer limbs. This may mean the light expected to pass between the cone outer limbs is not really wasted or, to put it differently, that it is collected and passes through the light-sensitive material (TANSLEY and JOHNSON, 1956; DARTNALL, 1960a).

Although it would be hazardous to speculate much further, one other point requires comment. If the inner limb changes the vergence of the light incident on the receptor then

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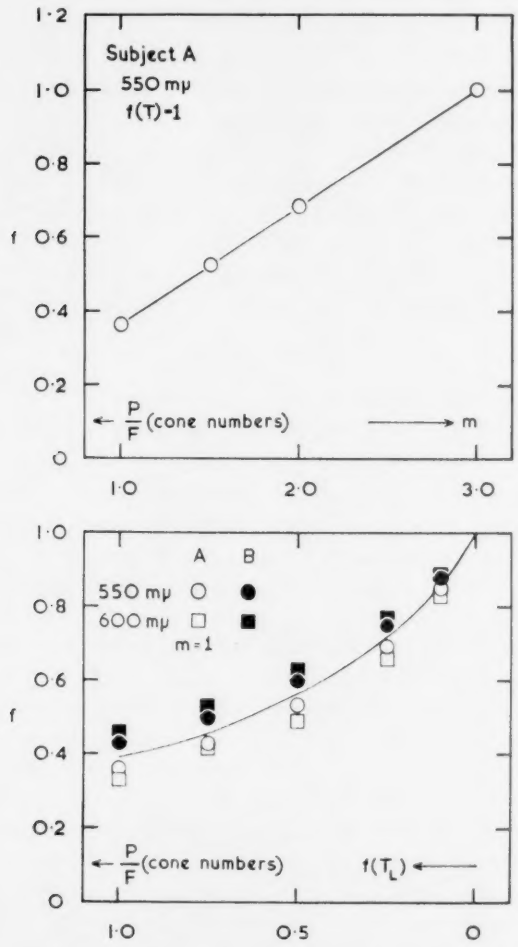

FIG. 13. Points calculated from equations (2) and (3). Estimates of the ratio of the effective receiving areas of extra-foveal and foveal cones respectively, as a function of the ratio of the lengths of the outer limbs (top), and the transmissivity of bleached pigment (bottom).

a distribution of light-sensitive material along the outer limb would be uneconomical. This suggests that, to a first approximation, the length of the outer limb does not govern the absorption of light. Now we have seen that the minimum ratio of the photo-sensitivities of the extra-foveal "chrome" pigments and visual purple is about 3·6. This value was arrived at on the assumption that the ratio of the effective cross-sectional areas of peripheral cones and rods was about 11, receptor for receptor. According to POLYAK (1941), the ratio of the total cone inner segment area at 8°N to its foveal counterpart is about $\frac{1}{2}$ ((f) in Fig. 13). Reference to Fig. 13 shows then that (m), the calculated ratio of the lengths of foveal to non-foveal cone outer limbs, is only a little over 1 instead of the histological value of 6. Thus on the basis of the above simple theory, the rather sparse data are compatible with the view that the length of the cone outer limb is not much involved densitometrically in the absorption

characteristics of cones, and support the belief that the light-sensitive material is concentrated in a volume smaller than that of the outer segment.

This would explain several phenomena. The change of vergence due to the inner segment would help without raising the bogey of too many internal reflections. The variation in refractive index in the neighbourhood of the outer segment membrane is unlikely to be large but any factor which increases the angle of incidence somewhat beyond the critical angle will be of use. The location of the pigment near the tip would also explain the extremely rapid regeneration of the "chrome" pigments when bleached. For KÜHNE (see FOSTER, 1878) has shown that contact between retina and pigment epithelium is essential even for the regeneration of visual purple. Clearly the less far metabolites have to diffuse the more rapidly will regeneration be completed.

The Density of Visual Purple in situ

The maximum density changes for double passage through the retina shown in the inset to Fig. 6 agree well with RUSHTON's (1956b) "irreducible" value of 0·156. However, in arriving at a value for single transit a number of factors had to be considered. Examining the ratio between density changes as measured for single and double transit, LEWIS (1956) obtained a value of 0·54 for the albino rat. Rushton used this value even though, in principle, this ratio can be determined easily enough in the living human eye. Again, as shown in Fig. 6, measurement in only one retinal location can lead to a severe underestimate of the retinal maximum. Quite clearly Rushton's data have only a partial bearing on the maximum in the retinae he examined, and less so on those of HECHT, SHLAER and PIRENNE (1942), whose data he attempts to explain, but who measured thresholds in a region somewhat different from that examined by Rushton. What he has shown and what the present data confirm is that the *in situ* density is higher than has been estimated on the basis of the properties of retinal extracts (CRESCITELLI and DARTNALL, 1953). But it would be surprising if the effective density were twice as high as Rushton's estimate of 0·15. The past mis-application of LUDVIGH and MCCARTHY's (1938) pre-retinal correction factor (WEALE, 1961a) and uncertainties in the scotopic visibility curve (WALD and BROWN, 1958) vitiate any closely reasoned argument based on the shape of such a curve. In agreement with Rushton, it may be said that HECHT, SHLAER and PIRENNE's (1942) estimate of the number of quanta required at the absolute visual threshold is consistent with the present density measurements, as indeed it was shown to be from a consideration of kinetics (cf. p. 374).

Some Sensory Aspects

The fact that the maximum effective density change is comparable in magnitude for the fovea and periphery (Fig. 4) agrees well with the observation that, measured with small fields, the absolute thresholds in these regions are comparable (BAUMGARDT, 1949; ARDEN and WEALE, 1954; WEALE, 1958b; RIEZLER, ESPER and MEURERS, 1954). The difference between the thresholds of foveal and extra-foveal cones (WALD, 1958) is easily accounted for in terms of cone-density (WEALE, 1960), but less so if lengths of outer limbs and focusing of light by the cone inner segments play a role. Thus the peripheral cone threshold as measured with small fields is some 1·5 log units higher than the foveal cone value. Differences due to the effective light flux reduce this value to 1·2, and the fact that only one type of cone is likely to operate under threshold conditions (STILES, 1939) to approximately 0·7. It

remains to be settled whether or not this discrepancy is due to the non-validity of the hypotheses here advanced, or e.g. to the peripheral cones being inhibited by rods (DODT and JESSEN, 1960).

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TROUGH HEIGHT, PRESSURE AND FLATTENING IN TONOMETRY[1]

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Abstract—Our automatic, gentle, electronic tonometer which is based on an exact theory yields a characteristic tonogram. We have shown in a previous paper that the initial crest occurs when the transducer surface is just covered by the flattened cornea and that the trough occurs when it is more than covered. Using rabbit eyes, the relationship was investigated between the degree of flattening and the intraocular pressure by electronic manometry and cannulation. Then the change in manometric pressure was found at the incidence of the initial trough of the Mackay–Marg tonogram. It is demonstrated that a 1½-mm diameter circular transducer surface area requires a 3-mm diameter flattening of the cornea for the generation of the initial trough. The artificial rise in pressure caused by this applanation is 0·4 mm Hg.

Résumé—Notre tonomètre automatique, léger et électronique, fondé sur une théorie exacte, fournit un tonogramme caractéristique. Nous avons montré précédemment que le ressaut initial se produit quand la surface du palpeur est juste couverte par la cornée aplatie et que le creux se produit quand elle est plus que couverte. On a étudié sur des yeux de lapin la relation entre le degré d'aplatissement et la pression intraoculaire avec une canule et un manomètre électronique. On a alors trouvé que le changement de pression manométrique coïncidait avec le creux initial du tonogramme de Mackay–Marg. On a démontré qu'un palpeur circulaire de 1,5 mm de diamètre nécessite un aplatissement de la cornée de 3 mm de diamètre pour engendrer le creux initial. Cet aplatissement produit une augmentation artificielle de pression de 0,4 mm de mercure.

Zusammenfassung—Unser automatisches elektronisches Tonometer, das auf exakter Theorie beruht, liefert ein charakteristisches Tonogramm. In einer früheren Arbeit haben wir gezeigt, dass das erste Maximum im Tonogramm auftritt wenn die abgeflachte Cornea eben den Stempel des mechanoelektrischen Wandlers bedeckt und dass die Kurve wieder abfällt, wenn die Cornea auch das Führungsrohr des Stempels berührt. An Kaninchenaugen wurde durch elektronische und direkte Druckmessung die Beziehung zwischen dem Grad der Abflachung und dem intraokulären Druck untersucht. Dabei ergab sich, dass die Änderung des Manometerdrucks dem ersten Minimum des Mackay–Marg-Tonogramms entspricht. Es wird gezeigt, dass für einen Wandlerstempel von 1,5 mm Durchmesser ein cornealer Abflachungsbereich von 3 mm Durchmesser erforderlich ist, um das erste Minimum zu erzeugen. Die durch diese Abflachung hervorgerufene artefizielle Drucksteigerung beträgt 0,4 mm Hg.

OUR NEW automatic, gentle, electronic tonometer yields in less than a second a characteristic tonogram (Fig. 1) from which the intraocular pressure may be read (MACKAY and MARG, 1959, 1960a and b; MACKAY, MARG and OECHSLI, 1960). The reading is free from sizeable errors inherent in other tonometers because of its unique design. It has been shown, in accordance with an exact theory, that the initial trough height above the base line gives the measure of the pressure within the eye (MACKAY and MARG, 1960b; MACKAY, MARG and OECHSLI, 1960; MARG, MACKAY and OECHSLI, 1961).

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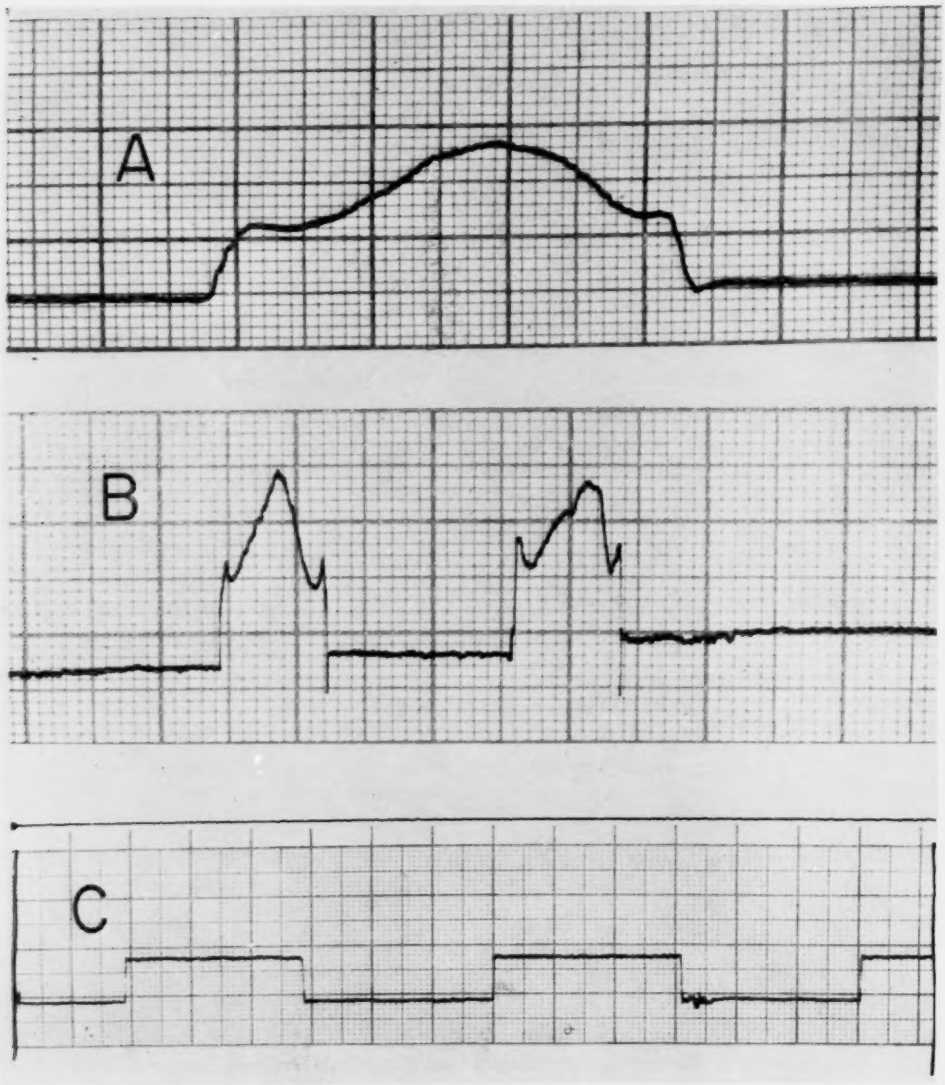

FIG. 1. Mackay–Marg tonograms from the human eye showing the initial crest, initial trough, central maximum and second trough and crest. The intraocular pressure is measured from the initial trough to the base line. The height of the crest above the trough is a measure of corneal stiffness. Chart speed, 2 large divisions or 10 mm/sec.

A. Tonogram taken with slow movement of probe taking over 3 sec overall. Initial trough obtained in 0·6 sec.

B. Two tonograms taken in rapid succession. Initial trough obtained in 0·1 sec so that the slight temperature drift indicated by rise of base line is not of significance.

C. Square wave calibration obtained by shifting the tonometer probe from vertically pointed down to up and repeat (+ and − one gravity). The amplifier may be set for any desired sensitivity. In this instance 1 mm on the chart equals 3 mm Hg (±g = 24 mm Hg).

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We have previously established that the crest occurs when the transducer surface is just fully covered (MACKAY and MARG, 1960b; MACKAY, MARG and OECHSLI, 1960; MARG, MACKAY and OECHSLI, 1961). We also have pointed out that the trough occurs when the transducer surface is more than covered by the cornea. How much more has been unknown up to this time. The purpose of this paper is to establish quantitatively the diameter of the flattened corneal surface at the occurrence of the first trough or plateau. In addition, we wish to determine quantitatively the artificial rise in pressure when various diameters of the cornea are flattened. The increase in pressure at the moment of the development of the initial trough is of special interest for tonometer calibration.

TONOMETER PRINCIPLE

It may be well to review, briefly, the principle and theory of our tonometer. If a low compliance transducer of, say 1½-mm diameter is set flush into a flat plate, one has a unique tonometer. Fig. 2 illustrates the sequence of events as the transducer surface is progressively covered, and more than covered, by the flattened cornea. The trough occurs when the bending forces of the cornea are no longer pushing on the transducer surface but on the surrounding, non-sensitive, coplanar area. In the same way the surface tension forces of tears are also avoided as an artifact in the reading. Corneal astigmatism is of no consequence since only the pressure from the central part of the flattened area is registered. Eye size, condition of the epithelium and ocular rigidity are of no significance nor is the orientation of the subject. Tissue tension forces are tangential in the flattened area so that first order theory dictates that the trough height gives only the intraocular pressure, less a correction for the rise in pressure caused by the volume change from applanation at the moment the first trough appears. The data providing this small correction value will be examined presently. It should be mentioned that the tonometer probe tip is covered by a thin rubber film (receptacle-end condom) to prevent the transfer of infectious eye diseases from one patient to another. It also keeps the tonometer dry and clean and presents a uniform and smooth surface to the cornea. A thin layer of petroleum jelly over the rubber film keeps it from imbibing water and makes the use of the tonometer without anesthesia more comfortable. The probe may be applied in any orientation and the reading is equally valid as long as it is not shifted between the initial contact and the initial trough, a fraction of a second. The response of the probe to gravity constitutes a built-in calibration device which makes the tonometer calibration independent of amplifier gain and other variable factors.

EQUIPMENT AND PROCEDURE

Tonometer

This investigation was performed with a form of the tonometer without mechanical feedback as illustrated in Fig. 3.[2] A highly sensitive differential transformer was used. It had a sensitivity of 100 μV output for each volt-micron input. The core was extended to provide a 1½-mm diam. circular area flush with a surround which measured 5-mm diam. overall. Both the transducer core extension and the surround were made of quartz and invar—materials with very low temperature coefficients to minimize temperature transients. The core was potted in silicone rubber which acted both as a bearing and a stiff spring. The spring action was so stiff that the displacement of the transducer in response to pressure was 250 Å/mm Hg, similar to that in previous models of the tonometer with mechanical feedback. This permitted the elimination of a complex feedback mechanism, while maintaining the principle and function of the earlier model. In a phrase, essential co-

[2] This instrument is manufactured by Biotronics, Inc., 405 14th Street, Oakland 12, California. Patent pending: Regents, University of California.

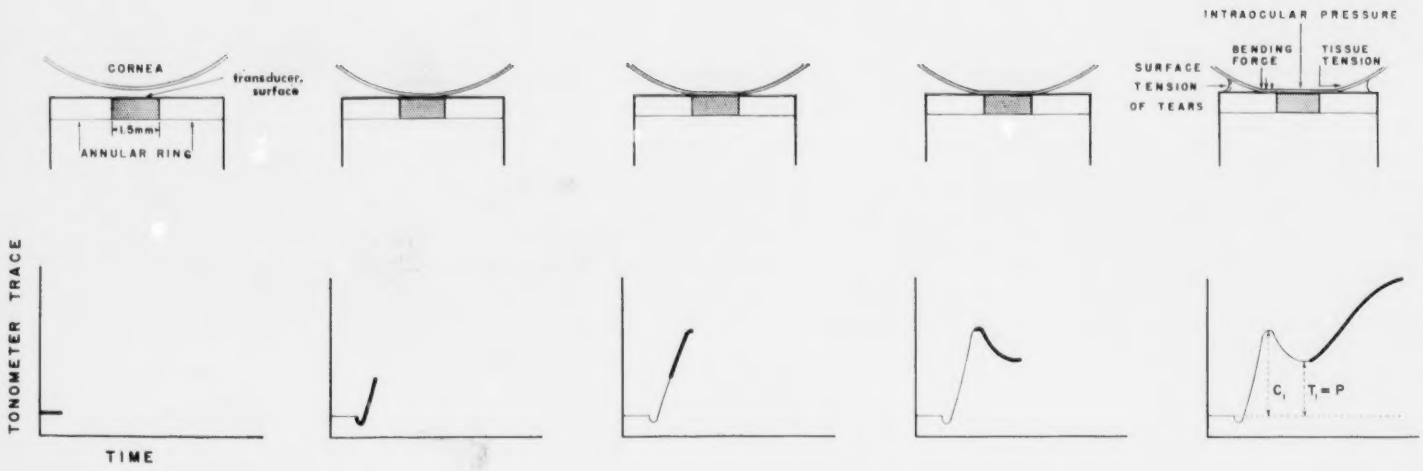

FIG. 2. The sequence of events as the tonometer probe is advanced towards and on the cornea. Note that as the flattening is increased the trough occurs when the bending forces of the cornea are transferred beyond the sensitive transducer surface to the coplanar surrounding insensitive area or annular ring. C_1 = initial crest; T_1 = initial trough which yields the intraocular pressure, P. Occasionally a tiny initial and final dip from the base line is noted, as shown, because of surface tension attracting the plunger before or after actual contact.

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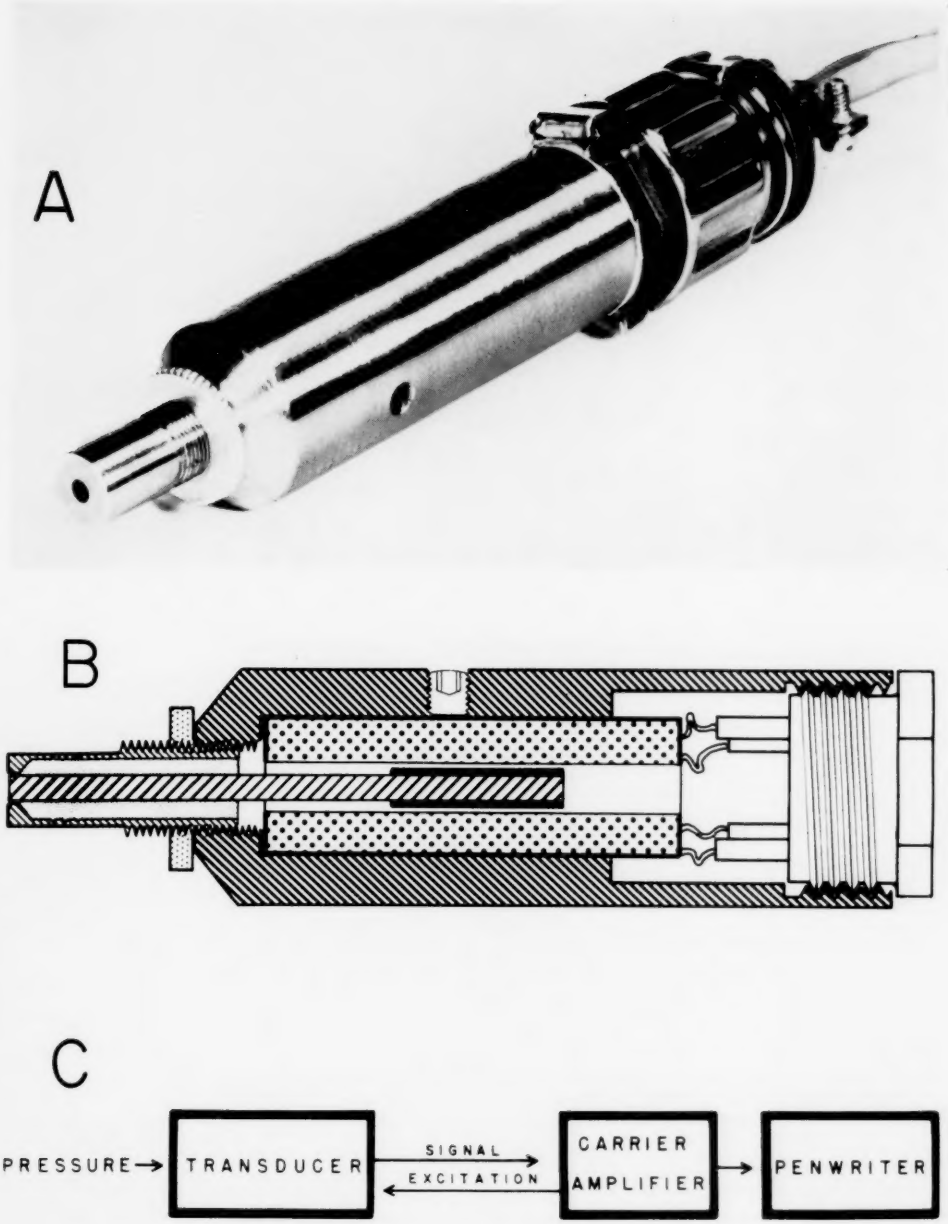

FIG. 3. A. Tonometer probe with 1½-mm diam. transducer surface in the center of the tip (for details, see text).

B. Cross-sectional drawing of tonometer probe construction (for explanation, see text).

C. Scheme of tonometer function. Penwriter must be reasonably fast for clinical application, with a frequency response extending to approximately 100 c/s.

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planarity was maintained. The output of the tonometer probe was fed into a carrier-amplifier recorder of adequate sensitivity and frequency response from which the tonogram was obtained.

In more recent models, a "grain of wheat" lamp in the probe provides a beam of light issuing from the transducer surface which may aid in centering the instrument on the cornea.

Electronic Manometer

The pressure of the eye during tonometry was measured by a Lilly electronic manometer (Technitrol Engineering Co., Philadelphia) because its transducer has an insignificant displacement of 1×10^{-7} ml/mm Hg. The output signal of the radio frequency bridge manometer was fed to a standard pen-recorder. Calibration was accomplished by the usual measured water column.

Procedure

A 20-gauge hypodermic needle was inserted into the anterior chamber of a rabbit eye *in situ*. The needle was connected to the transducer of the electronic manometer by a fine, thick-wall polyethylene tube. After the puncture, the eye was restored to normal pressure by means of a water manometer reservoir, or, if the animal were alive, allowed to regain its normal pressure. A polished truncated cone of transparent plastic was advanced toward the eye by means of a micrometer screw until its small end flattened the cornea. By dropping India ink on the cornea, the degree of applanation was clearly seen with good contrast and was photographed for subsequent measurement with a 35-mm camera fitted with an electronic flash. During this time the electronic manometer was continuously recording the pressure.

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Various degrees of flattening were produced. Exact values for each of the diameters of the flattened area and the rise in pressure elicited by this flattening were recorded simultaneously. Then the tonometer, registering on a second channel of the recorder, was applied to the eye and the increase of pressure registered by the electronic manometer was noted at the time the trough or crest appeared. These data allowed comparison of the degree of flattening at the time of the trough or plateau by relating it to the same rise in pressure for the previous measurements. An earlier fruitless attempt was made to measure the flattening and the tonometer value simultaneously. A specially designed "transparent" tonometer was constructed so that the flattening could be photographed, but it was not transparent enough to obtain accurate measurements of the diameter. The method finally used was perhaps less elegant but, what is more important, was successful.

RESULTS

The curve displaying diameter of corneal flattening versus rise in pressure is shown in Fig. 4. It is evident that the pressure starts to rise rapidly in the vicinity of a 3-mm diam. area. One may plot on the curve the rise in pressure at which the troughs or plateaus are found with the tonometer. The triangles in Fig. 3 show that it is about 0·4 mm Hg. This demonstrates that the tonometer with a $1\frac{1}{2}$-mm diam. circular transducer surface area employs a total flattening of 3-mm diameter for the reading of the intraocular pressure.

DISCUSSION

At first glance it may appear that a 3-mm diam. flattening is quite a large extension beyond the sensitive area. A moment's consideration makes it clear that beyond the $1\frac{1}{2}$-mm diam. transducer area there lies an annulus of flattened cornea only $\frac{3}{4}$-mm wide. The bending forces of the cornea must be so distributed that they reach a minimum over the transducer

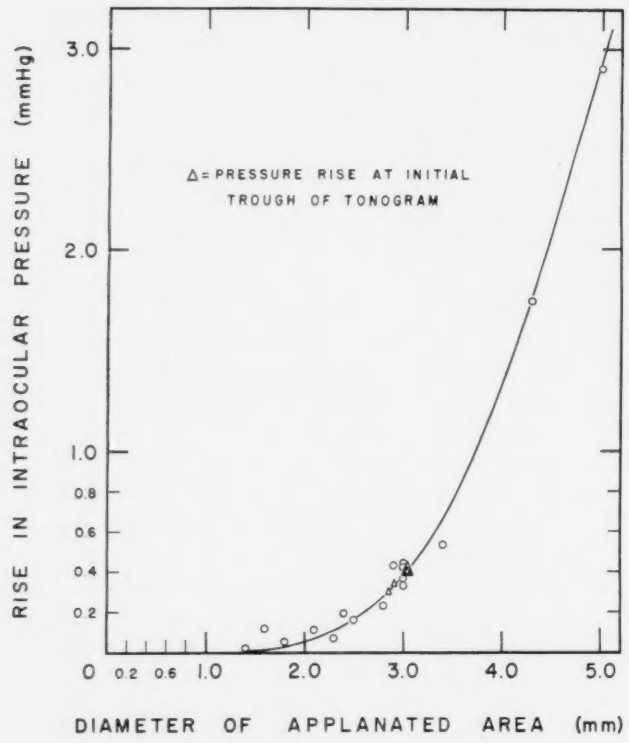

FIG. 4. The rise in intraocular pressure for various amounts of flattening of a rabbit eye. Several tonograms were taken and the rise in intraocular pressure at the moment of the trough is represented on the curve as triangles. Note that it requires 3-mm flattening to obtain the initial trough with a 1½-mm diam. circular transducer surface area.

in relation to the climbing intraocular pressure when they are maximally about ¾ mm away. This value appears reasonable for a corneal thickness of ½–¾ mm.

A rise of 0·4 mm Hg of pressure at the trough indicates that this value should be subtracted in the calibration of the tonometer probe when made by open manometric tests, i.e. when the pressure within the eye or other hydraulic chamber is maintained regardless of volume changes. The small differences in calibration found among various mammalian species with our tonometer (MOSES, MARG and OECHSLI, 1962) would indicate that this finding is probably valid for other mammalian eyes as well as for those of rabbits.

It is likely that there will be a slightly different actual rise in pressure in eyes with different ocular rigidities and basic pressures. However, the 0·4 mm Hg correction is probably accurate enough for any absolute measurements of pressure for which tonometry can be used. Relative measurements in the same eye would be even less affected.

The curve showing the relationship between change of pressure and diameter of flattened area in Fig. 3 was obtained from a freshly dead rabbit eye *in situ*. Several other similar experiments gave the same results. When the data were obtained from a living rabbit eye, two differences were noted. First, there was much greater scatter of points, presumably largely caused by the moment-to-moment changes of pressure due to the pulse. Second, the

curve was not exactly the same shape, undoubtedly because of the effects of homeostatic or feedback regulation of pressure and perhaps some differences in ocular rigidity. However, the results from freshly dead animals were the same as from the live animals; the trough occurred at a 3-mm diam. flattening.

Some rabbit eyes exhibit little or no crest. This must mean that the corneal stiffness is less than in those rabbit or other eyes in which a sharp crest is observed. The stiffer and the thicker the cornea, the greater the flattening required to reach the trough. This small second or third order correction is of theoretical interest only and may be ignored in clinical measurements.

SUMMARY

The relation between the diameter of flattening and manometric change of intraocular pressure was found and graphed. The change in manometric pressure was determined at the point where the initial trough appears in a Mackay–Marg tonogram. Comparison of these data shows that with a 1½-mm diam. transducer surface diameter the cornea is flattened to an area of 3-mm. diameter when the first trough appears on the tonogram.

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THE MECHANISM OF DARK-ADAPTATION

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Abstract—An analysis is given of the various possible components of the dark-adaptation process. A distinction is made between: *Photochemical* component (f_1), *neural receptor* component (f_2), *spatial summation* component (D), *temporal summation* component (T) and a *quantum coincidence* component (k). These various components partly reveal themselves in different ways in dark-adaptation curves obtained by sensitivity measurements as a function of time for different target-sizes, different target-colours and different retinal locations.

Experiments were carried out in order to study the relative contribution of each component for foveal as well as for peripheral vision.

Foveal adaptation appears to be governed by the component f_1 and perhaps also f_2. In phase I of peripheral adaptation a small D-component is added and in phase II of peripheral adaptation only the k-component is active.

The behaviour of the resting potential of the human eye during dark-adaptation does not bear a simple relation to any of the neural components mentioned in the present paper.

Résumé—On analyse les diverses composantes possibles du processus d'adaptation à l'obscurité. On distingue: une composante *photochimique* (f_1), une composante du *récepteur nerveux* (f_2), une composante de *sommation spatiale* (D), une composante de *sommation temporelle* (T) et une composante de *coincidence quantique* (k). Ces diverses composantes sont partiellement mises en évidence de plusieurs façons dans les courbes d'adaptation à l'obscurité obtenues par la mesure de la sensibilité en fonction du temps pour différentes dimensions de tests, différentes couleurs de tests et différentes positions sur la rétine.

On a réalisé des expériences dans le but d'étudier la contribution relative de chaque composante pour la vision fovéale ainsi que périphérique.

L'adaptation fovéale semble gouvernée par la composante f_1 et peut-être aussi par f_2. Dans la phase I de l'adaptation périphérique, il s'ajoute une petite composante D et dans la phase II de l'adaptation périphérique la composante k est seule active.

Le comportement du potentiel de repos de l'oeil humain durant l'adaptation à l'obscurité ne présente de relation simple avec aucune des composantes nerveuses mentionnées dans le présent travail.

Zusammenfassung—Es wird eine Analyse der verschiedenen möglichen Bestandteile des Prozesses der Dunkeladaption gegeben. Eine Unterscheidung wird gemacht zwischen: einer photochemischen Komponente (f_1), einer Nerven-Receptor-Komponente (f_2), einer räumlichen Summations-Komponente (D), einer zeitlichen Summations-Komponente (T), und einer Quantenkoinzidenz-Komponente (k). Diese verschiedenen Komponenten zeigen sich zum Teil auf verschiedene Weise in Dunkeladaptionskurven, welche durch Messungen der Empfindlichkeit als Funktion der Zeit für verschiedene Scheibengrössen, Scheibenfarben, und Netzhautlagen erhalten wurden.

Es wurden Experimente durchgeführt, um den relativen Beitrag jeder Komponente sowohl für das zentrale als auch für das periphere Sehen zu studieren.

Die foveale Adaption scheint durch die Komponente f_1 und vielleicht auch durch f_2 bestimmt zu werden. In der Phase I der peripheren Adaption kommt ein kleiner D-Anteil hinzu, während in der Phase II nur die k-Komponente wirksam ist.

Das Verhalten des Ruhepotentials des menschlichen Auges während der Dunkeladaption ergibt keine einfache Beziehung zu irgendeiner der in dieser Abhandlung aufgeführten Nerven-Komponenten.

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1. INTRODUCTION

SINCE the publication of the classical experiments of AUBERT (1865) on dark-adaptation an impressive amount of psychophysical measurements has been carried out on the human eye and it would appear that the experimental material would suffice to allow us to draw some theoretical conclusions on the mechanisms underlying this interesting and important phenomenon.

From the beginning it was accepted that peripheral, presumably retinal, mechanisms were largely or completely responsible for the decrease of the absolute threshold in the course of dark-adaptation, a decrease which amounts to a factor 10^5 under the most favourable experimental conditions (pre-adaptation to white light at a high intensity level; a large test field, presented to the peripheral parts of the retina). The mere fact that the state of dark-adaptation of one eye is independent of the state of dark-adaptation of the other eye has always been one of the strongest arguments in favour of peripheral mechanisms of dark-adaptation. Another strong argument for purely retinal mechanisms of dark-adaptation has arisen from electrophysiological work on the human eye. It has been shown by several investigators that the change of the *b*-wave of the human ERG in the course of dark-adaptation closely follows the change of the absolute threshold as determined by means of psychophysical methods.

Thus if we try to give a theoretical interpretation of the phenomena of dark-adaptation we must focus our attention on the retina. Our knowledge of the objective properties of the retina can be classified under the following headings:

(A) Anatomy,
(B) Photochemistry,
(C) Neurophysiology (including electrophysiology).

(*A*) *Anatomy*

The most important contribution of anatomy towards understanding the phenomena of dark-adaptation is without any doubt the "duplicity theory" formulated in its final form by VON KRIES (1896).

The wealth of arguments in favour of the concept that the human retina contains two receptor mechanisms, which act to a large degree independently of each other, is so overwhelming that we may accept its validity as an established fact.

A number of other anatomical observations, mainly pertaining to retinomotoric phenomena like pigment migration and contraction of the outer lids of the cones, although very interesting from a physiological point of view, have hardly influenced our theoretical concepts of human dark-adaptation owing to the fact that they are mainly observed in lower vertebrates and are not demonstrable in the human eye.

(*B*) *Photochemistry*

The discovery of the photochemical bleaching of rhodopsin by BOLL (1877) and the stream of subsequent work in this field largely influences the theories of dark-adaptation up to the present day.

The fact that the rods contain a visual pigment with a spectral absorption which is nearly similar to the spectral sensitivity of the dark-adapted eye, combined with the fact that the concentration of rhodopsin increases during dark-adaptation, makes it attractive to consider whether the increase of the concentration of rhodopsin in itself is sufficient to

explain the decrease of the absolute threshold (the increase of sensitivity) during the course of rod-adaptation. The discovery of another pigment, iodopsin, by WALD (1937) with a spectral absorption which is supposed to represent the photopic sensitivity curve of the human eye and with a *time* course of regeneration *in vitro* which is nearly identical to the *time* course of human cone-adaptation opens a similar perspective for a photochemical theory of cone-adaptation.

Such a photochemical theory of dark-adaptation would be easily acceptable if it could be shown that the increase of sensitivity during cone- and rod-adaptation is directly proportional to the increase of the concentration of iodopsin and rhodopsin, respectively (if we assume that these photopigments are present in a diluted solution), or more briefly formulated that for any particular moment of dark-adaptation

$$\text{for cone-adaptation } C_i = K_i S \tag{1}$$
$$\text{for rod-adaptation } C_r = K_r S \tag{2}$$

in which formulae S denotes the sensitivity of the eye (the reciprocal of the absolute threshold) at a certain moment, K_i and K_r are constants which are characteristic for the iodopsin and the rhodopsin systems, C_i and C_r are the concentrations of iodopsin and rhodopsin.

This simple theory, which suggests that the visual pigment is present in the receptor cell in the form of a dilute solution and that the sensitivity is the subjective correlate of the probability of the absorption of a light quantum by the receptor cell, is in direct conflict with an abundance of experimental evidence which shows that the increase of the concentration of rhodopsin during dark-adaptation is much smaller than the corresponding increase of the sensitivity of the eye.

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HECHT (1929) made the assumption, based on experiments on the clam, *Mya*, that at any moment of dark-adaptation the logarithm of the sensitivity is directly proportional to the logarithm of the concentration of the visual pigment or in formulae

$$\text{for cone-adaptation } C_i = K_i \log S \tag{3}$$
$$\text{for rod-adaptation } C_r = K_r \log S \tag{4}$$

in which formulae K_i and K_r are constants characteristic for the cone and rod systems.

Hecht has shown that the acceptance of the conditions (3) and (4) makes it possible to describe the course of human dark-adaptation by means of the "dynamics of a bimolecular reaction isotherm". He thus concluded that "during dark-adaptation the photopigment is being replenished in the rods and in the cones independently as if in each case it were being formed by the chemical interaction of at least two other substances".

WALD (1955) is still convinced of the validity of the relations (3) and (4). He believes that "light- and dark-adaptation have their primary source in the bleaching and resynthesis of the visual pigments of the rods and cones". However, he believes that "more central phenomena-changes in the sensitivities of neurones and synapses along the optic pathway may also play a role. . . . They probably are responsible also for only a minor portion of the range of visual adaptation. To a first approximation light- and dark-adaptation seem to reflect the fall and rise of visual pigment; and specifically in the form that the log sensivity runs parallel with pigment concentration."

From this quotation we learn that Wald is forced to admit that the full range of dark-adaptation cannot be explained by photochemistry alone. Recently some strong arguments against a purely photochemical explanation of dark-adaptation have arisen. BAUMGARDT (1949) and others have calculated that the number of quanta absorbed in the rods at

moderate illumination levels is too small to cause an appreciable change in the concentration of rhodopsin.

RUSHTON and CAMPBELL (1954) developed a method which made it possible to measure the change in the density of rhodopsin in the living human eye. They established that "unless fairly bright photopic illumination is used, there is no appreciable change in the density of retinal rhodopsin. Thus changes in visual sensitivity cannot be due to an alteration in the chance of a quantum being absorbed; it must be entirely due to a change in the efficacy of the quantum when it is absorbed."

From this quotation we may conclude that RUSHTON and CAMPBELL (1954) go so far as to deny a photochemical mechanism of dark-adaptation. Recently it has been made clear by WALRAVEN and BOUMAN (1960) that the change in apparent hue when the light enters the pupil through more eccentric parts is due to a shortening of the pathway of the incident light through a fairly concentrated solution of the photopigment in the receptor. According to their explanation of this aspect of the Stiles–Crawford effect such a dependence of apparent hue on the site of entrance of the light in the pupil would disappear when the concentration of the photopigment became small. However, only for very high brightness levels did BRINDLEY (1953) find such an effect.

In any case it seems clear that a purely photochemical theory of dark-adaptation does not meet the experimental facts and we will have to consider the possible existence of neural mechanisms if we wish to explain the experimental data.

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(*C*) *Neurophysiology*

The existence of neural mechanisms of dark-adaptation does not only follow in an indirect way from the failure of the photochemical theories to explain all phenomena of dark-adaptation but also in a direct way from psychophysical experiments on the human eye.

Many investigators have shown that the *range* of adaptation increases with an increase of the test-field area. We mention here BEST (1950), BOUMAN and TEN DOESSCHATE (1953) and ARDEN and WEALE (1954). This effect can be partly explained by an increase of the diameter of the area of complete integration during dark-adaptation (ARDEN and WEALE (1954)) which clearly represents a neural mechanism of dark-adaptation. BOUMAN and TEN DOESSCHATE (1953) have shown that the effect can also be ascribed to a change of the critical number of coincident quanta (a concept which will be discussed in the next sections), thus indicating another neural mechanism. In the older literature several authors have considered neural mechanisms of adaptation, e.g. LYTHGOE (1940), CRAIK and VERNON (1941) and THOMSON (1949).

The most direct argument in favour of neural components of adaptation stems from electrophysiological work on the eye of *Limulus*. HARTLINE (1957) reported about his adaptation experiments on the *Limulus*-eye. He determined "frequency of spike curves" for different adaptational conditions.

The microelectrode was situated in the visual apparatus in such a position that at least one synaptic connection had to be passed by the response on its way to the higher centres. He measured the probability of occurrence of at least one spike response as a function of the intensity of flashes presented to the *Limulus*-eye. He found that the "frequency of spike curves" can exactly be described by the formula

$$W(\bar{N}, k) = 1 - e^{-f\bar{N}} \sum_{o}^{k-1} \frac{f\bar{N}^{p}}{p!}$$

in which $W(\bar{N}, k)$ is the probability that for an average number of quanta $\bar{N}$ in an actual flash, k effective quantum absorptions occur as predicted by Poisson's distribution of statistical events and f is the fraction of the incident light that is absorbed in the photopigment. HARTLINE (1957) found that for different conditions of adaptation different k-values are valid. The f-value, however, was the same for all curves. His k-values varied between two and about 100. This important change of the value of k with the state of adaptation points to the importance of a nervous component in dark-adaptation. It is indeed the same effect which was found for the human eye by BOUMAN and TEN DOESSCHATE (1953). It also seems important that Hartline's shallowest curve corresponds to $k=2$, the same number which was found by BOUMAN and VAN DER VELDEN (1947) for the dark-adapted human eye.

Hartline's very objective studies by means of electrophysiological methods show that this property of the human eye should be considered as a general property of visual receptor systems.

2. THEORETICAL ANALYSIS OF THE POSSIBLE COMPONENTS OF DARK-ADAPTATION

In order to facilitate the analysis of the different components of the process of dark-adaptation we want to introduce a system of terms and symbols:

Mechanism	Term	Symbol
(A) Increase of the concentration of the photopigment	photochemical component	f_1
(B) Neural-adaptation of the single receptor	neural receptor component	f_2
(C) Increase of the retinal summation area	area component	D
(D) Increase of retinal summation time	time component	T
(E) Decrease of the minimum number of coincident quanta	coincidence component	k

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Ad A *and* B—*Photochemical component and neural receptor component* (f_1 *and* f_2)

The sensitivity of the fully dark-adapted eye is so high that it is easy to prove that at the absolute threshold for short light flashes the chance that one receptor is hit by more than one quantum is negligible. The consequence of this statement is that the absorption of one quantum by an active molecule of photopigment is not only sufficient for the decomposition of one molecule of photopigment but that this decomposition is sufficient to produce a response of the receptor in the dark-adapted retina. An increase of the threshold in the light-adapted state could be explained by one of the following hypotheses:

(1) In the light-adapted eye *more than one* quantum is necessary for the decomposition of one molecule of photopigment. This hypothesis seems to be most improbable on physical and chemical grounds.

(2) In the light-adapted eye the concentration of photopigment is less than in the dark-adapted eye. This is the mechanism which we have called the *photochemical component* (f_1). We have seen in the preceding section that the importance of this component has been overestimated in the past. However, assuming that this mechanism is present, it will be clear that an increase of the concentration of active

photopigment during dark-adaptation will result in an increase of the probability that an active molecule is hit by a quantum of incident light radiation.

(3) The fact that the absorption of one quantum by one active molecule is *sufficient* to cause a response of the receptor does not mean that *every* absorption results in an effective spike response.

If we call the probability that an absorption will result in an effective spike response p per cent, we may consider the possibility that the value of p is less for the light-adapted eye than for the dark-adapted eye even under the condition that the concentration of the photopigment remains unaltered. This possible mechanism we have denoted by the term *neural receptor component* (f_2).

Both components f_1 and f_2 have a very simple effect on the threshold of the eye. They act in the same way as if a filter is removed from before the eye. The influence of this factor is independent of the area of the test field (d^2) or from the duration of the stimulus (t).

Ad C *and* D—*Area component* (D) *and time component* (T)

It is a well-known fact that two subliminal point stimuli will be able to produce a supraliminal response if they are applied within a critical distance (D) and within a critical duration (T). The critical distance is generally considered to coincide with the area of validity of Ricco's law of complete spatial summation. The critical duration T covers the time within which Bloch's law of complete temporal summation is valid. It will be clear that an increase of D or T respectively during the course of dark-adaptation will result in an increase of the probability of a supraliminal response. These effects are denoted here as *area component* (D) and *time component* (T) respectively. Their real existence has been shown by means of experiment (VAN DER BRINK and BOUMAN, 1954; ARDEN and WEALE, 1954).

Ad E—*Coincidence component* (k)

It has been shown by several investigators that the phenomena at the visual threshold level are governed by relatively simple quantum-statistical considerations. We assume that the retina is stimulated by a circular test field with diameter (d) during a time (t). A visual response will be elicited if a critical number of quanta (k) is effectively absorbed within a critical area with diameter (D) and within a critical time (T). This simple hypothesis allows us to apply Poisson's formula to the theoretical treatment of the problem. Experimental data on the behaviour of the probability of a visual response as a function of the stimulus intensity, the diameter of the test field (d) and the duration of the stimulus (t) can be explained by assuming that for the dark-adapted eye $k=2$. The authors of the present paper (BOUMAN and TEN DOESSCHATE (1953)) have shown that for the light-adapted eye $k=>2$. The variation of k with the state of adaptation represents a neural mechanism of dark-adaptation which we have denoted by the term *coincidence component* (k).

From the considerations given above we may conclude that of the different components of dark-adaptation the first one (f_1) is purely photochemical in origin. All others should be classified as neural components. The f_2 component is a relatively simple neural component belonging to the single receptor. The other neural components (D, T and k) have a more complicated character. The common characteristic of this group of mechanisms is a change of the switching arrangement within *groups* of receptors during the course of dark-adaptation.

In the discussion of the experiments which will be described in the next section much attention is given to the behaviour of the threshold energy of a test flash as a function of its diameter (d). It will clarify the discussion if we describe, in advance in a very schematic way, the theoretical influence of the different components of dark-adaptation on this function.

In order to simplify our arguments still further we will assume that under all circumstances $t<T$. By accepting this condition we eliminate the T-component of dark-adaptation from our arguments.

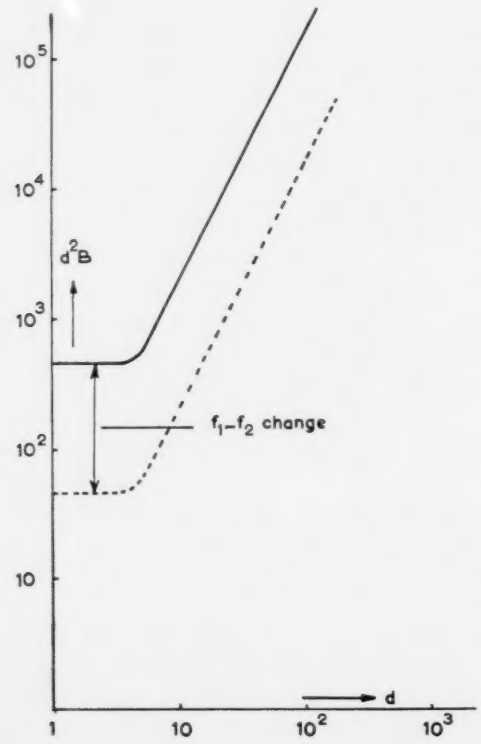

FIG. 1. Effect of f_1 or f_2-component on the function $d^2B_{threshold}=f(d)$.

In Fig. 1 the upper (drawn) line gives the threshold energy d^2B of a test flash with diameter (d) as a function of (d) or in a shorter notation

$$d^2B_{\ threshold} = f(d).$$

(In this function B is the threshold *luminance* of the test flash.)

We observe that the function consists of two distinct parts, on the left a horizontal part and on the right a part with a positive slope. The left horizontal part covers the range of d values within which complete spatial summation occurs or in other words the range for which $d<D$. The second part of the function (the part with a positive slope) corresponds to the condition $d>D$. (We will see below that the slope of this part is determined by the critical number of coincident quanta k. In Fig. 1 the slope is quite arbitrarily drawn for $k=20$.) The lower function (dotted line) shows the effect of an increase of the concentration

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of active photopigment (f_1-component) by a factor 10 (the value 10 is quite arbitrarily accepted) but the same effect is obtained if the spike-efficiency of the individual receptor (f_2-component) increases by a factor 10.

In Fig. 2 the effect of an increase of the area of complete spatial summation (D^2) by a factor 10 (or an increase of D by a factor $\sqrt{10}$) is shown. The effect of the D-component becomes apparent as soon as d exceeds the original value of D (dotted line). The curve assumes a positive slope for large d-values with k again 20.

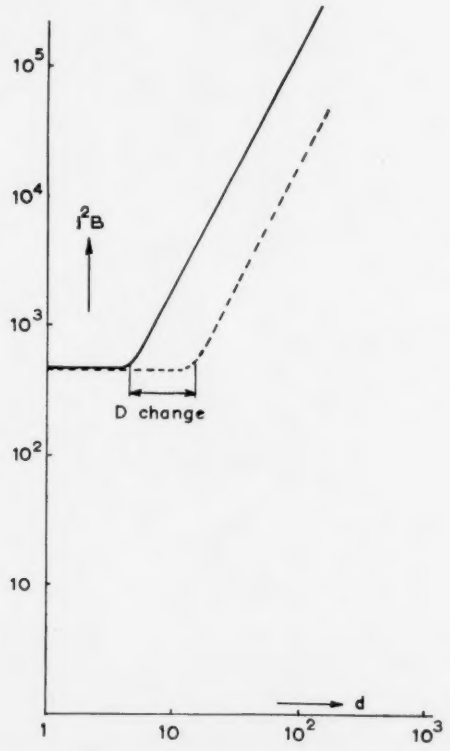

FIG. 2. Effect of D-component on the function $d^2B_{threshold}=f(d)$.

The effect of the T-component need not be considered here for we assumed that $t<T$ under all circumstances.

In Fig. 3 we show the effect of a decrease of k by a factor 10 on the function $d^2B_{\ threshold} = f(d)$.

Earlier it has been shown by BOUMAN and VAN DER VELDEN (1947) that the positive slope of the function is proportional to

$$d^{2(k-1)/k}$$

The upper (drawn) function is drawn for $k=20$ (slope $=+38/20$). The lower (dotted) line represents $k=2$ (slope $=+1$).

The results obtained from Figs. 1–3 may be summarised in the following way:

(1) Effect of f_1 and f_2-component: A lowering of the threshold by a "filter"-factor which is independent of d.

(2) Effect of D-component: No effect as long as $d<D$. An increasing effect over the range within which d exceeds the original value of D but has not reached the final value of D. After d exceeds the final value of D, the effect remains constant.

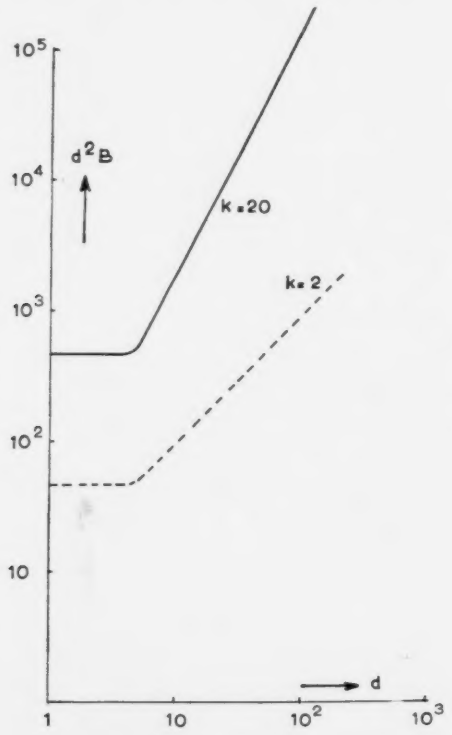

FIG. 3. Effect of k-component on the function $d^2B_{threshold}=f(d)$.

(3) Effect of k-component: A constant effect for $d<D$. This effect is proportional to k. An increasing effect for $d>D$.

Figure 4 combines the results from Figs. 1–3 and thus represents the combined effects of the different components of dark-adaptation on the function $d^2B=f(d)$.

3. EXPERIMENTAL

(1) *Introduction*

In the preceding section we have shown that an experimental study of the threshold energy of test flashes as a function of the state of dark-adaptation and the diameter (d) of the test field and for small duration of the test flash ($t<T$) offers interesting possibilities for an analysis of the different components which may play a part in the complicated process of dark-adaptation.

It was our aim to study the mechanism of dark-adaptation for rod- and cone-adaptation separately as far as possible. Therefore, we were obliged to carry out threshold determinations for red and green test fields which were presented to the fovea as well as to the periphery during the complete course of dark-adaptation. In order to obtain maximum adaptation effects an extremely high level of pre-adaptation to white light was adopted. By means of this device we hoped to give all components their fullest chance to present themselves.

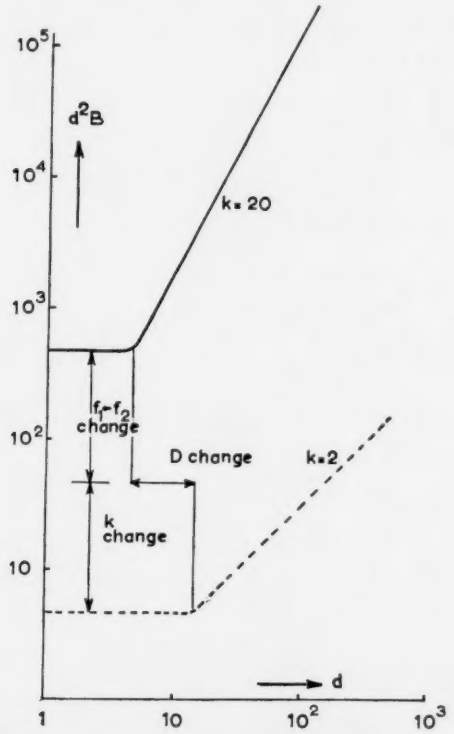

FIG. 4. Combined effect of the different components on the function $d^2B=f(d)$.

(2) *Experimental Procedure and Apparatus*

All experiments were carried out on the right eye of a well-trained forty-year-old male observer. (The right eye of the subject is myopic (2 *D*) and shows a mild degree of deuteranomaly.)

In all experiments the subject was pre-adapted during 3 min to a field with diameter 18° which was observed in Maxwellian view through an artificial pupil with diameter 2 mm. The pre-adaptation light was obtained in the following way: the artificial pupil coincided with the image of a tungsten ribbon filament lamp which was run at 14 A. At this current strength the lamp has a colour temperature of 2848°K. The luminous flux passing through the artificial pupil was experimentally determined and amounted to 0·125 lumen. The luminance of the adapting field was equivalent to about $5{\cdot}5\times10^5$ cd/m^2, corresponding to a retinal illumination of $2{\cdot}2\times10^6$ trolands. The pre-adaptation period was followed by a 30-min period of

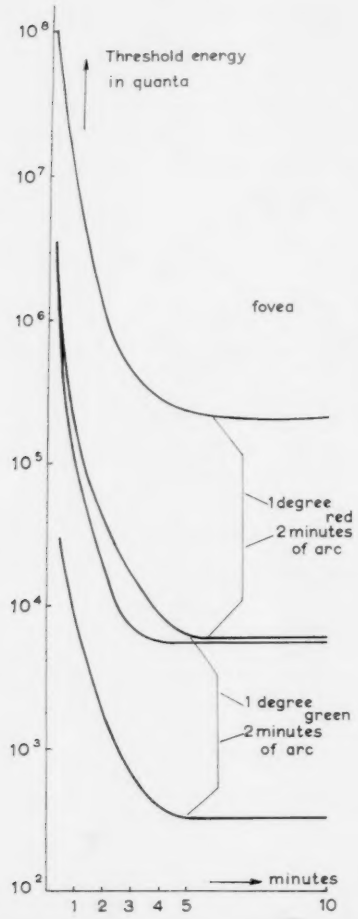

FIG. 5. Results for red and green, fovea. Curves averaged from five independent measurements.

dark-adaptation. During this latter period the threshold energy of a test flash was determined at small intervals. A 50 per cent chance of observation was considered to be the threshold level.

The curves presented in Figs. 5–7 were obtained from the experimental data in the following way:

The current running through the tungsten ribbon filament lamp was recorded by means of a recording ammeter. Every light flash which was observed by the subject was recorded on the same paper by means of an electrical signal. As soon as the probability of seeing reached more than 50 per cent the current was reduced by a certain amount and remained at its new level until the probability of seeing at this new level was again more than 50 per cent. This procedure was repeated during the complete course of dark-adaptation.

Afterwards the 50 per cent probability-of-seeing curves were marked in the finished records and smooth lines were drawn through the experimental 50 per cent points. For

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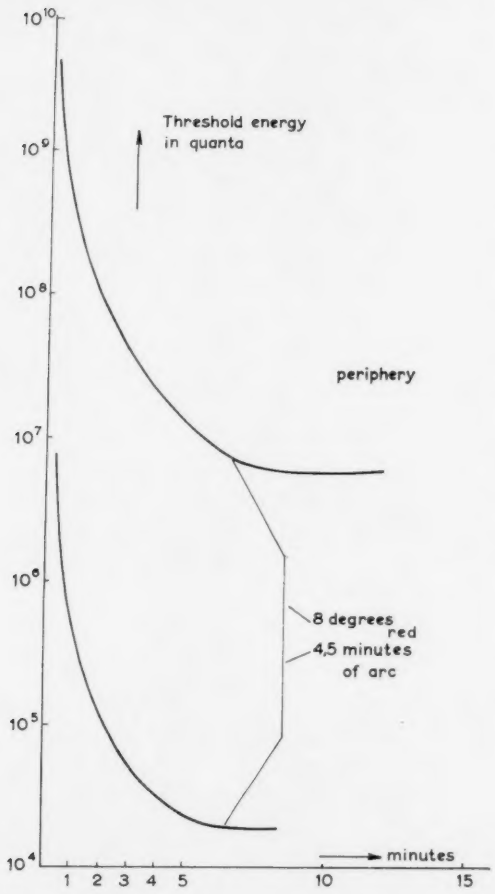

FIG. 6. Results for red light, periphery. Curves averaged from five independent measurements.

every experimental condition we carried out at least five completely independent experiments. The records obtained in these five experiments were averaged by means of graphical interpolation. The interpolation curve still represented lamp current against time of adaptation. By means of the calibration data of the lamp, the filters and the monochromator, the average current data were converted into radiant energy (expressed in quanta). The curves in Figs. 5–7 are the result of this graphical interpolation.

From the foregoing description of the experimental procedure it will be clear that in Figs. 5–7 no experimental points are given. The curves should be considered as smooth curves drawn through a very large number of experimentally determined points. The spread of the values did not exceed a standard deviation of about 70 per cent.

The curves are comparable to classical curves of dark-adaptation which are also used for clinical reasons. In these clinical procedures, however, the curves represent the log *threshold luminance* as a function of the time of dark-adaptation. In the curves presented in this section the log *threshold energy* (luminance multiplied by area of the test field) is plotted as a

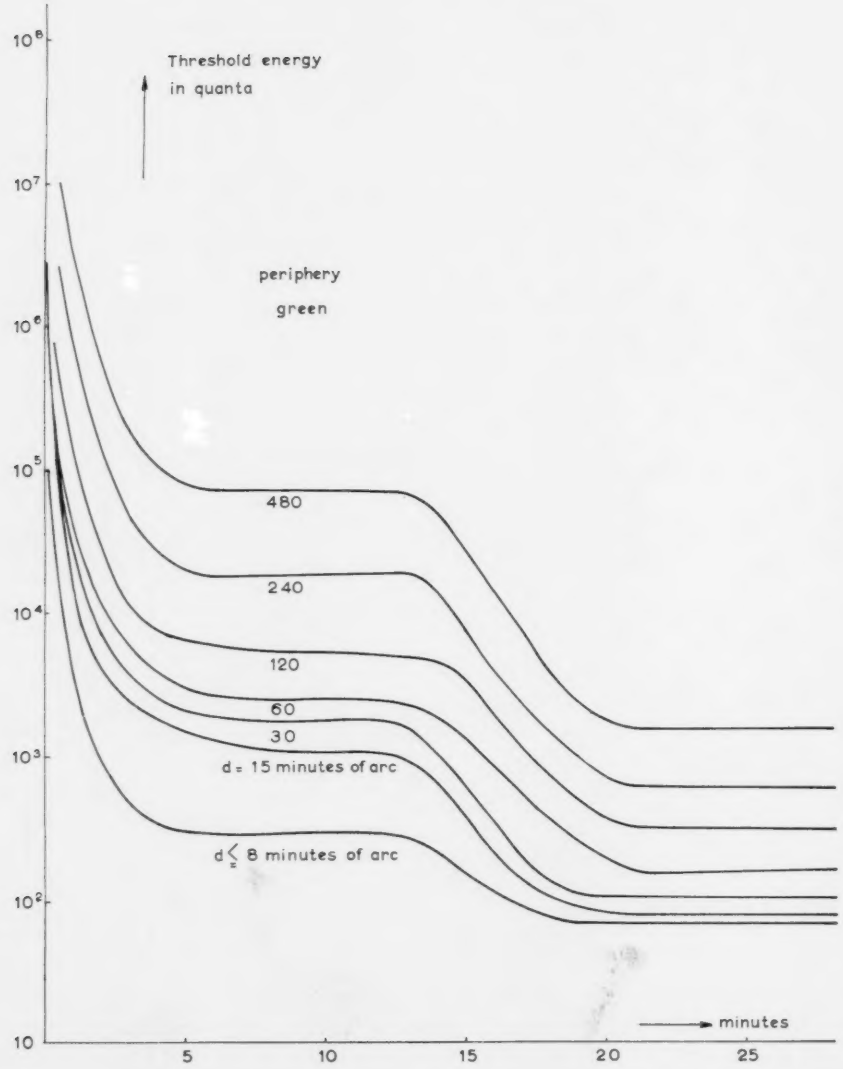

FIG. 7. Results for green light, periphery. Curves averaged from five independent measurements.

function of the time of dark-adaptation. Experiments were carried out for red (650 mμ) and green (525 mμ) test flashes with duration 0·1 sec presented to the fovea or to the periphery (7° temporal of the fovea). The diameter of the test field ranged from 1·9′–1° for the foveal and from 1·9′–8° for the peripheral measurements. The test field was also observed in Maxwellian view through the artificial pupil (2 mm). The colour of the test field was varied by means of a double monochromator adjusted at a maximum band width of about 25 mμ. The luminance of the test field was continually varied by adjusting the current

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strength of the light source of the monochromator and discontinually by means of a set of neutral filters. All thresholds energies in this section are expressed in quanta.

(3) *Experimental Results and Discussion*

In Fig. 5 we give the experimental data for the fovea for red and green test flashes plotted as log threshold energy as a function of the time of dark-adaptation and for different diameters (d) of the test flash.

In order to be able to interpret these figures one should consider the theory presented in section 2.

Similarity of the *shape* of the curve for small and large test fields excludes the possibility that D or k-component are active. Such a similarity can only be explained by the activity of the f_1 and/or the f_2-component. The foveal measurements presented in Fig. 5 clearly fulfil this condition for red as well as for green test flashes, showing that foveal-adaptation is completely governed by photochemical and/or neural receptor adaptation. The total amplitude of foveal-adaptation amounts to a factor which is about equal to 100. From the curves presented here no conclusions can be drawn with respect to the relative contribution of the f_1 and the f_2-component. From other sources of information mentioned in section 1 we know that foveal dark-adaptation cannot be explained by means of the f_2-component alone. It has been shown by Brindley that the difference in optical density of the photopigment in the light- and the dark-adapted fovea is sufficient to cause a difference in the shape of the spectral absorption curve. If we assume that in the dark-adapted fovea the maximum absorption by the photopigment is about 50 per cent, a decrease to maximum 10 per cent is needed to account for the required change in the shape of the spectral absorption curve in the light-adapted eye (see also WALRAVEN and BOUMAN (1960)). We may thus conclude that foveal dark-adaptation is at least partly due to the f_1-component.

We may now proceed to the analysis of the peripheral measurements.

From Figs. 6 and 7 we learn that for small test fields ($d<4{\cdot}5'$) and within the first 12 min of dark-adaptation for red as well as for green test flashes the situation can be simply described by stating that the shape of the curves is within the margin of experimental error similar to the shape of the foveal curves. This result strongly suggests that for small test fields in the periphery during the first 12 min of dark-adaptation the cones alone are responsible for the increase of the sensitivity. Furthermore, we may conclude that in this respect the peripheral cones are identical to the foveal cones. Summarizing, we may conclude that the curves describing foveal-adaptation and the first phase of peripheral-adaptation for small test fields for red as well as for green are all identical. Under these conditions adaptation is governed by the cones only and the mechanisms concerned are only the f_1 and perhaps the f_2-component.

For large test fields the situation is much more complicated. For a red 8° test field the curve is monophasic and at the first glance its form seems to be identical with that of the foveal curves and the peripheral curves for small test fields. A closer examination reveals that the range of adaptation for the red 8° field exceeds the range for the 4·5′ red field by a factor 2. In order to explain this discrepancy the activity of one of the neural components (D or k) has to be taken into consideration. (We will see below that the effect is probably due to the D-component.)

The curves for green test fields in the periphery (Fig. 7) all clearly show a diphasic form, thus presenting the well-known "break" of the curve for dark-adaptation which is classically

ascribed to the transition of cone- to rod-adaptation. Perhaps some reader will be surprised by the fact that the "break" is so pronounced and that it shows itself not earlier than the twelfth minute of dark-adaptation. This fact is easily explained by considering the unusually high level of pre-adaptation ($2{\cdot}2 \times 10^6$ trolands).

In discussing the results (Fig. 7) we will refer to the two phases of the curve as phase I and phase II. Phase I for the curve for 8° green (Fig. 7) is identical in form to the peripheral curve for 8° red (Fig. 6). Here also we find that the amplitude of phase I of the 8° curve

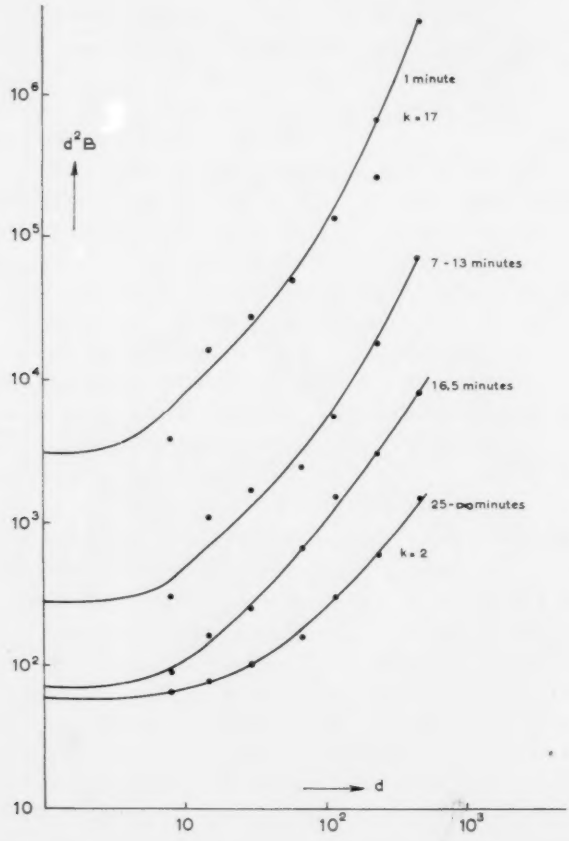

FIG. 8. $d^2B = f(d)$; peripheral measurements for green light at different levels of dark-adaptation.

between the first and eighth minute of dark-adaptation exceeds that of the small field curve by a factor 2. Here also the effect must be explained by the activity of the D or k-component (and again it will be shown below that it is probably due to the D-component).

From Fig. 7 we learn that for phase II of the green curves the amplitude of adaptation increases appreciably if the diameter (d) is increased from 7·5′ to 8° (i.e. 480′). This clearly indicates that part II of the curves for peripherally presented green test fields is governed to a large extent by neural components (D and/or k). We have seen in section 2 that it is

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possible to separate the effect of these components by studying the behaviour of the threshold energy as a function of d. Therefore we give in Fig. 8 vertical sections of the set of curves presented in Fig. 7.

The curves given in Fig. 8 show log threshold energy (d^2B) as a function of d. Each curve pertains to a certain moment of dark-adaptation. The slope of the curve between 1 and 12 min of dark-adaptation appears to correspond to k = about 17. At the end of dark-adaptation the slope corresponds to $k=2$. We may state therefore that in phase II of dark-adaptation the k-effect should amount to a factor $17/2 \approx 8$. This change in k value ought at least to appear in phase II of the curves for small fields in Fig. 7. From this figure we learn that for small

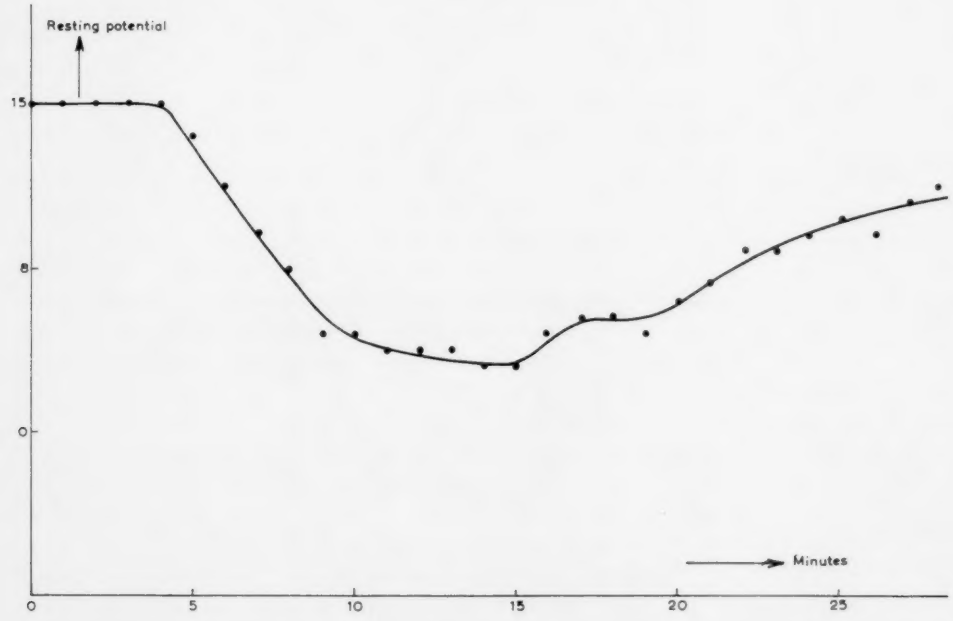

FIG. 9. Resting potential as a function of the time of dark-adaptation for the same subject on whom all experiments in the present paper were carried out and with the same conditions of pre-adaptation.

fields ($d<8'$) the amplitude of adaptation in phase II of the curve amounts to a factor 6. Thus the range of adaptation during phase II is nearly completely explained by the decrease of k. We may conclude that phase II of the peripheral dark-adaptation curve is governed by the k-component only and that in this phase f_1, f_2 and D-component are absent. Furthermore, from the fact that the k-component is "spent" completely on phase II of dark-adaptation we may conclude that the neural component in phase I must be the D-component.

It means that in phase I, D changes approximately by a factor $\sqrt{2}=1{\cdot}4$. We mentioned already the relatively small variations in D as found by VAN DER BRINK and BOUMAN (1954) by more direct experiments. They were indeed of the same order of magnitude as deduced from the present experiments.

We may summarise our conclusions about the mechanisms of dark-adaptation in the following scheme:

Foveal-adaptation	f_1 at least a factor 5
	perhaps f_2 but if so not more than a factor 20
Peripheral-adaptation	
in phase I	f_1 at least a factor 5
	perhaps f_2 but if so not more than a factor 20
	D approximately a factor 1·5
in phase II	k-component by a factor 6 to 8

4. THE RELATION BETWEEN NEURAL COMPONENTS OF ADAPTATION AND THE RESTING POTENTIAL OF THE HUMAN EYE

TEN DOESSCHATE and TEN DOESSCHATE (1956, 1957) have shown that the resting potential of the human eye as determined from the amplitude of the electrooculogram behaves in a complicated way in the course of dark-adaptation. They suggested the possibility that this behaviour of the resting potential is the objective correlate of the activity of neural-adaptation. In order to test this hypothesis we determined the behaviour of the resting potential of the observer on whom the experiments described in the present paper were carried out. The pre-adaptation level was also identical to that which was used in the threshold experiments.

In Fig. 9 we give the resting potential as a function of the time of dark-adaptation.

From a comparison between Fig. 9 and Fig. 7 we learn that the resting potential is constant during the steep decrease of the threshold in phase I. The resting potential drops during that part of phase I in which the threshold is more or less constant. The resting potential reaches a minimum at the point of transition from phase I to phase II. It increases slowly during phase II. Apparently there is no simple relation between the behaviour of the resting potential during dark-adaptation and the different neural components of dark-adaptation.

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AN APPARATUS FOR THE INVESTIGATION OF CHROMATIC ADAPTATION[1]

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Abstract—An apparatus for measuring the visual changes that follow chromatic adaptation is described. It consists of a monochromator and a trichromatic colorimeter. The monochromator presents an adapting stimulus to the left eye of the observer in alternation with simultaneous exposures of test and matching stimuli to the left and right eyes, respectively, from the colorimeter. A special attachment provides the modifications required for monocular measurement.

The stimuli are monochromatic in that they comprise small bands of the visible spectrum. Auxiliary sources give high level luminance for stimuli taken from the far ends of the spectrum.

The controls of the colorimeter automatically retain the luminance at a relatively constant level while the observer varies the percentages of the components. This arrangement also provides equal luminance primaries. The procedures and techniques used for wavelength and luminance calibration of the apparatus are described.

Résumé—On décrit un appareil destiné à mesurer les modifications visuelles consécutives à une adaptation chromatique. Il consiste en un monochromateur et un colorimètre trichromatique. Le monochromateur présente à l'oeil gauche de l'observateur un stimulus d'adaptation qui alterne avec des expositions simultanées, fournies par le colorimètre, du test à l'oeil gauche et des stimuli de comparaison à l'oeil droit. Un dispositif spécial permet aussi les mesures monoculaires.

Les stimuli sont monochromatiques, en ce sens que ce sont des bandes étroites du spectre visible. Des sources auxilliaires fournissent des stimuli de luminance élevée pour les extrémités du spectre.

Le colorimètre maintient automatiquement la luminance à une valeur relativement constante lorsque l'observateur modifie les proportions des composantes. Cet arrangement fournit aussi des primaires d'égales luminances. On décrit les méthodes et techniques utilisées pour calibrer l'appareil en longueur d'onde et en luminance.

Zusammenfassung—Es wird eine aus einem Monochromator und einem trichromatischen Farbmessgerät bestehende Apparatur zur Messung der chromatischen Adaptation beschrieben. Dem linken Auge wird ein Adaptationsreiz aus dem Monochromator geboten. Damit abwechsend werden beide Augen gleichzeitig mit Test- und Mischreizen aus dem Farbenmischer erregt. Eine besondere Anordnung liefert die für eine monokulare Messung verlangten Modifikationen.

Die monochromatischen Reize bestehen aus schmalen Bändern des sichtbaren Spektrums. Zusätzliche Lichtquellen geben den Reizen aus den Spektrumsenden ein hohes Leuchtdichteniveau.

Der Farbmischer sorgt automatisch für ein relativ konstantes Leuchtdichteniveau, während der Beobachter den Prozentsatz der Komponenten ändert. Diese Anordnung liefert auch Primärvalenzen gleicher Leuchtdichte. Es wird das Verfahren für die Wellenlängen- und Leuchtdichteeichung der Apparatur angegeben.

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[1] This apparatus was developed under the successive auspices of the American Academy of Optometry, The Ohio State University Research Foundation, and the Office of Naval Research (Contr. Nonr-1056[00]).

[2] Now at the North American Aviation, Inc., Columbus, Ohio.

INTRODUCTION

THE APPARATUS described herein consists of a trichromatic colorimeter and a separate monochromator which provides an adapting stimulus from any region of the visible spectrum. It has been designed for the study of chromatic adaptation and the results of such studies will be presented in subsequent papers.

The colorimeter gives test and matching stimuli that are mixtures of spectrally pure[3] components. It is based upon the general design of the one developed by WRIGHT (1947). A new type of reflector has been substituted for greater convenience in controlling luminance. The apparatus provides equal luminance primaries and the luminance of the test and matching stimuli are retained at a relatively constant level while the observer varies the percentages of the components. Special auxiliary sources offer the same level of luminance for stimuli at the ends of the visible spectrum as at the middle. Also the various beams passing through the head of the instrument have been kept segregated to permit good control of the stray light.

THE STIMULI

The adapting stimulus from the monochromator is circular and subtends a maximum angle of 5°. Smaller stimuli of any desired configuration may be obtained by substituting metal inserts at the proper location in the apparatus.

The colorimeter provides a uniformly illuminated square stimulus area of $5 \times 5°$ subtense to each eye. Only a portion of this area is used, however, as shown in Fig. 1. A semicircular area and a fixation point are presented to the left eye to function as the test stimulus (A).

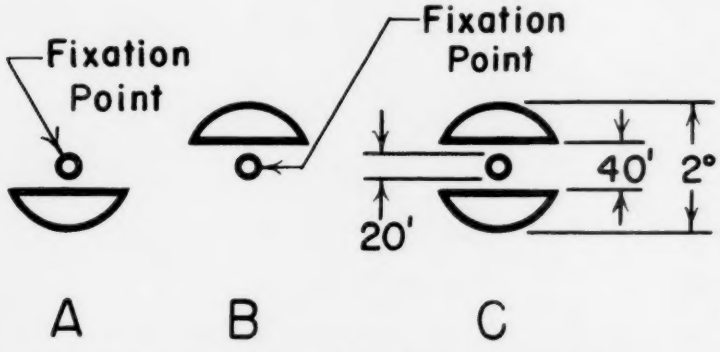

FIG. 1. Configurations of the test and matching stimuli.

The same configuration is inverted for presentation to the right eye as the matching stimulus (B). The binocular arrangement (C) thus involves fusion of the monocular fixation points and has a total angular subtense of 2°. It provides a highly stable configuration, which retains the spatial relations shown throughout a lengthy period of adaptation. Weak ophthalmic prisms can be used to aid in the maintenance of fusion.

[3] The terms *spectrally pure* and *monochromatic* are used here to designate narrow bands of the spectrum, such as those obtained with an ordinary monochromator.

These stimuli are presented on a dark surround. The test and matching stimuli are first simultaneously exposed to provide the binocular arrangement shown in Fig. 1. A color match is then obtained on the test stimulus, under standard conditions of adaptation. The adapting stimulus is then presented to the left eye for eight seconds with the test and matching stimuli removed from view. Following this, the adapting stimulus leaves the field as the test and matching stimuli return for 2 sec. This cycle is repeated again and again while the observer modifies the matching stimulus in both chromaticness and brightness during the 2-sec exposures so as to approximate the appearance of the changing test stimulus. The percentages of the matching components are then recorded when a stable match is obtained.

THE APPARATUS

The colorimeter is essentially symmetrical for the two optical systems carrying light beams to the right and left eyes of the observer, i.e. the beams that furnish components for the matching and test stimuli, respectively. We shall first trace the different beams of the colorimeter. The optics of the monochromator will then be discussed.

A. The Optical System of the Colorimeter

The three levels of the optical system of the colorimeter are diagrammatically presented in Figs. 2, 4 and 5. Fig. 2 shows the first level. Light from the main source A[4] is collimated

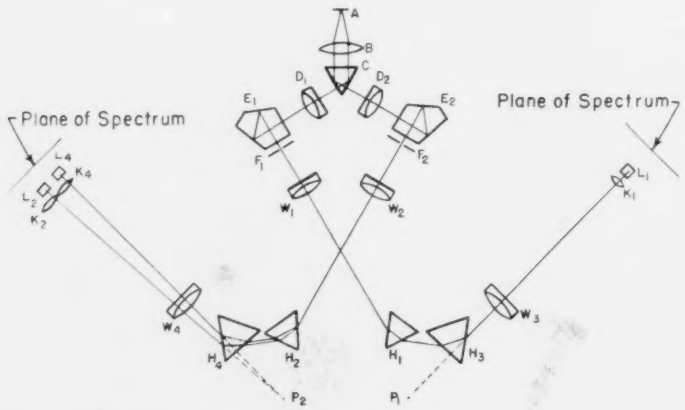

FIG. 2. First tier of the optical system.

by the lens B before it enters the equilateral prism C. This prism divides the light into two components, one directed to the entrance slit F_1 and the other to F_2.[5] The two beams are focused on their respective slits by the achromatic lenses D_1 and D_2. The pentaprisms E_1 and E_2 serve to change the direction of these beams through 90° from the central axes of the respective lenses, directing them to the centers of the slits. The slit F_1 furnishes one beam

[4] This is a 100 W, 6 V, General Electric vertical ribbon filament lamp (18A/T10/1 microscope illuminator), operated from an appropriate constant voltage transformer. These sources have an average color temperature of 2950° K when operating under normal conditions.

[5] The F_1 slit is variable in width from 0 to 1 mm, while F_2 is fixed at 1 mm.

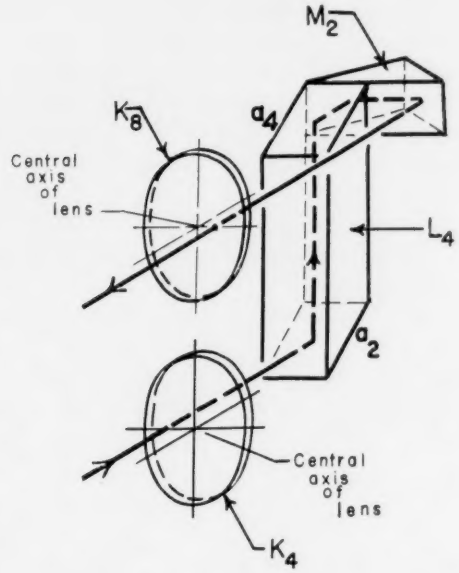

FIG. 3. Reflector unit.

for the test stimulus and the slit F_2 provides two beams for the matching stimulus. In order to facilitate the discussion to follow, the optical units transmitting the beams to the left eye have been given odd-numbered subscripts, while even numbers are attached to those for the right eye system.

Referring to Fig. 2, we see that the beam from the slit F_2 is directed to the dispersing prism H_2 by means of an achromatic lens W_2, which functions as a collimating lens. The prisms H_2 and H_4 in combination with the achromatic lens W_4 form a spectrum in the plane indicated. K_4 is a field lens inserted in front of the rhomboid prism L_4, which reflects a segment of the spectrum upward to the second level of the optical system as shown in Fig. 3.

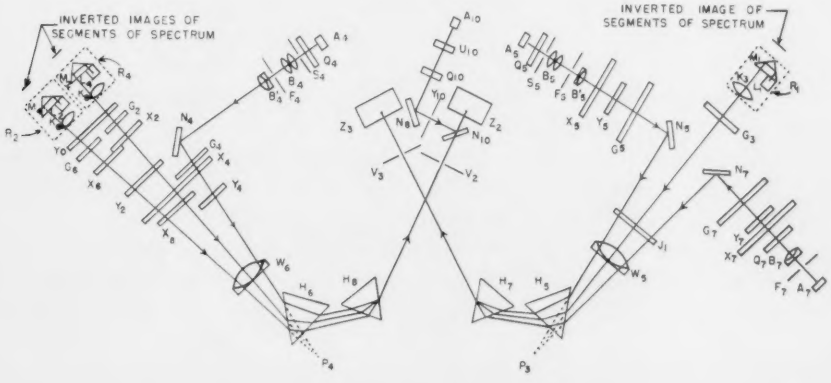

FIG. 4. Second tier of the optical system.

A Porro prism (M_2) is cemented to the back of the rhomboid so that the beam leaves this element in a direction exactly parallel to that from which it entered the rhomboid at the first level. It is then transmitted through a second field lens, K_8, which is located directly above K_4. This combination of lenses and prisms may aptly be termed a reflector, as it relays a segment of the spectrum to the second level, forming an inverted virtual image of it in a corresponding plane above the first level. The surfaces a_2 and a_4 are silvered so as to reflect the beam as shown.

Two of these reflectors are used in the right eye system and are schematically shown in Fig. 4 by the boxed areas designated R_2 and R_4. They may be moved along the spectrum, providing various monochromatic stimuli, or fixed, so as to comprise two components of a tristimulus system. These reflectors are on rolling supports which swing around a vertical axis through P_2 and P_4.

Fig. 4 shows the optical system of the second level of the apparatus. The light beams leaving the field lenses K_6 and K_8 of the two reflector units are combined into one by the

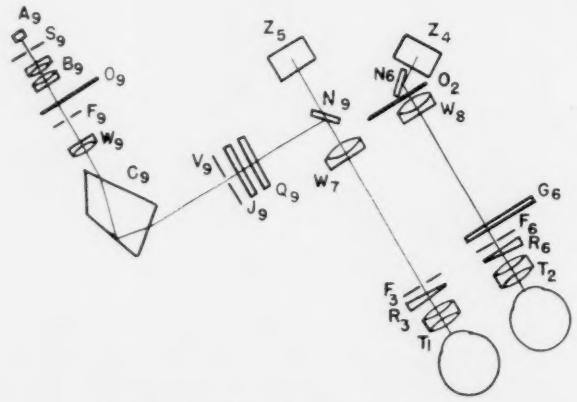

FIG. 5. Third tier of the optical system.

collimating lenses W_6 and the two prisms H_6 and H_8, which further disperse the beams. The combined beam is transmitted through the aperture in the diaphragm V_2, which constitutes the matching stimulus target, and on to the mirror Z_2, where its direction is changed upward through 90° so that it ascends to the third level of the optical system.

When the beam reaches the third level (Fig. 5), it is again deflected through 90° by another plane mirror (Z_4) so that it falls upon the mirror N_6. Here it is reflected through the angle required to center it upon the achromatic lens W_8 which is in turn centered upon the exit pupil F_6.[6] W_8 serves to focus the small segment of the spectrum picked up by the rhomboid prism L_4 (at the first optical level) in the plane of the exit pupil.

The stimulus target V_2 is placed in the focal plane of the lens W_8, and is therefore focused upon the retina of the observer's right eye. The slight prismatic correction given by R_6 is used to facilitate binocular fusion with the left eye stimulus. T_2 is a flint and crown glass

[6] The exit pupils of the colorimeter (F_3 and F_6) are 2 mm holes that are restricted laterally by 0·7 slit jaws and centered upon lenses W_7 and W_8. The range of wavelengths emerging from the exit pupils varies from about 3 mμ at 400 mμ to 25 mμ at 700 mμ.

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combination, which corrects for the axial chromatic aberration of the eye, but is afocal for 589 mμ.

An important aspect of the apparatus is shown in Figs. 2 and 4. The two lenses K_4 and K_8 make the point P_2 at the first level optically conjugate to P_4 of the second level. Components from the chief ray of a beam incident at the first face of prism H_2 emerge from the lens W_4 as if they diverge from P_2 to form the spectrum indicated in Fig. 2. The two segments of this spectrum that are redirected by the reflector units (R_2 and R_4) therefore converge toward P_4 and unite as they leave the second face of the prism H_8. This arrangement provides uniform illumination in the plane of the stimulus target V_2.

Brief mention may now be made of the optical system on the other side of the colorimeter, i.e. the one supplying the test beam for the left eye. It is essentially symmetrical with the system for the right eye just described and may be traced in an analagous manner. They differ in that the system for this side of the apparatus has only one reflector unit (R_1). This is usually used for the test beam. Attention is called to the test stimulus target V_3 which is the same as V_2 on the other side of the colorimeter except that it is inverted as shown in Fig. 1.

The sources A_4, A_5 and A_7 (Fig. 4) were installed because they provided greater luminance at the extreme ends of the visible spectrum than could be obtained from the beams of the colorimeter.

The A_4 source is a mercury lamp,[7] the light from which is stopped down by the diaphragm S_4 before it enters the condensing lenses (B_4) which focus it on the slit F_4. The beam is then directed to the lens W_6 by means of the mirror N_4. The lenses B_4 and B_4' place the image of the stop S_4 at P_4 which is conjugate to P_2 at the first optical level (Fig. 2). After the beam enters W_6 its path to the right eye of the observer is similar to that from the reflector of this side of the colorimeter, already described. This source gives a 436 mμ stimulus for use as one of the matching components.

The optical system of the A_5 source is identical with the A_4 source except that this source also furnishes a 405 mμ beam when the whole unit is swung around the point P_3. It is used both as a test stimulus and a desaturating component for other beams from this side of the colorimeter. Both mercury sources are filtered by Corning glass 5113 filters ($\frac{1}{2}$ standard thickness) to eliminate stray light.

The A_7 source has the same kind of vertical ribbon filament lamp as used with the main source of the colorimeter described above. It has the same optical system as the other auxiliary sources, except that condensing lenses are not used with it. The lens B_7, the mirror N_7, the lens W_5 and the prisms H_5 and H_7 together form an image of the ribbon filament at the stimulus target V_3. This source is used for obtaining a 680 mμ stimulus for the left eye. Q_7 is a 2408 Corning glass filter used to eliminate stray light from the green and blue regions of the spectrum.

The source A_{10} (Fig. 3) is a 7·5 W Mazda lamp which is used as a standard stimulus against which the luminance of the 530 mμ and 436 mμ matching components going to the right eye may be monocularly compared from time to time. A variac is used to control the luminance of this source, which is measured in terms of voltmeter readings.

The beam from the A_{10} source is intercepted by a piece of ground glass U_{10}, which diffuses the light before it passes through a 4303 Corning glass filter (Q_{10}) and the comparison stimulus target Y_{10}. An image of the target is formed by the mirror N_{10}, adjacent to the

[7] This is an H–4, 100 W, General Electric lamp, used with a special transformer and voltage regulator.

stimulus target V_2, giving a photometric bipartite stimulus configuration with a horizontal dividing line for this side of the colorimeter.

The monocular viewing apparatus (Fig. 6) mounts on the front of the colorimeter and is used for monocular comparisons of the stimuli presented to the two eyes. It provides a vertically oriented bipartite stimulus by combining the binocular stimuli from the colorimeter in the manner shown in Fig. 6.

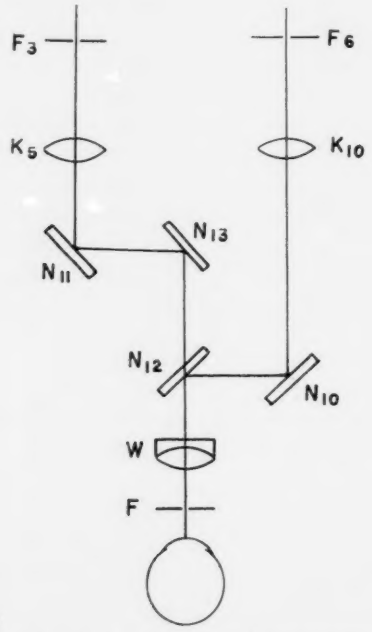

FIG. 6. The monocular viewing apparatus.

The exit pupils of the colorimeter (F_3 and F_6) are shown in Fig. 6 in the same manner as in Fig. 5. Images of the stimulus targets of the colorimeter are focused in the plane of the mirror N_{12} (which halves the field to give a horizontal dividing line) by means of the lenses K_5 and K_{10} respectively. The mirrors N_{10}, N_{11} and N_{13} serve to align the images in vertical juxtaposition, so that they may both be monocularly viewed through the achromatic lens W and focused upon the observer's retina. F is a circular aperture which assists the observer in aligning his eye properly, but it is large enough to transmit all of each of the two beams.

B. The Optical System of the Monochromator

The optical system of the monochromator is shown in Fig. 5. A_9 is a vertical ribbon filament lamp such as the one used for the main source of the colorimeter described above. Light from this source is stopped down by the diaphragm S_9 and focused on the slit F_9 by the condensing lenses B_9. It is then collimated by the lens W_9 and passes through the Pellin–Broca prism C_9. N_9 is a plane mirror which deflects the beam through 90°. The beam is therefore centered on the W_7 lens of the colorimeter when N_9 is properly positioned in the observer's left eye field of view.

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The spectrum formed by the prism is focused in the plane of the F_3 exit pupil of the colorimeter by the W_7 lens. The prism rotates around a vertical axis so that the spectrum can be repositioned, allowing a different segment to pass through the exit pupil[8] to the eye of the observer.

V_9 is a diaphragm which provides the adapting stimulus. It is located in the focal plane of the W_7 lens and is therefore focused upon the retina of the observer's eye.

An electrically powered gear mechanism controls the movement of N_9 in and out of the viewing field along a line perpendicular to the axis of the viewing unit of the colorimeter. With this arrangement, the adapting stimulus is viewed for 8 sec and is then removed for 2 sec while the stimuli from the colorimeter are observed. This cycle is repeated as long as desired.

O_2 is an occluder which moves with N_9 and covers the matching stimulus during the periods of exposure to the adapting stimulus. O_9 is also an occluder which cuts off the adapting beam whenever N_9 moves out of the viewing field.

A 5031 Corning glass filter is used in the monochromator for wavelengths below 490 mμ to reduce stray light from other regions. A 2030 filter is likewise used with wavelengths above 740 mμ.

THE LUMINANCE CONTROLS

The controls of the colorimeter automatically retain the luminance of the test and matching stimuli at a relatively constant level while the observer varies the relative proportions of the separate components. The initial luminance level of each component is set by neutral density wedges.

A. The Luminance Controls of the Matching Stimulus and its Components

Referring to Fig. 4 the three matching components presented to the right eye of the observer are 680 mμ (from reflector R_2), 530 mμ (from reflector R_4) and 436 mμ (from the A_4 mercury source). Other stimuli may be used in their place by repositioning the reflectors (or the mercury source) on an arc around the point P_4.

The maximum luminance of each component is set by varying the respective neutral wedges G_6, G_2 and G_4 to provide equal luminance primaries for measurement before adaptation. The neutral wedge G_8 (Fig. 5) is used to control the overall luminance of the matching stimulus. Under a standard set of adaptive conditions, this wedge is set for maximum transmission of the components.

The relative proportion of each component of the matching stimulus is controlled by pairs of polaroid filters: Y_2 and X_6 for the 680 mμ component, Y_2 and X_2 for the 530 mμ component and Y_4 and X_4 for the 436 mμ component. These are shown in Fig. 3. The "Y" polaroids are fixed and the "X" polaroids rotate.

The polaroid filters X_2 and X_6 are mounted on the same shaft, but are 90° out of phase and rotate together. Thus, when the 680 mμ component is increased by a given amount, the 530 mμ component is automatically decreased by about the same amount, merely by rotating a single knob and the total luminance of the stimulus is relatively unaffected.

The fixed polaroid Y_4 for the 436 mμ component is 90° out of phase with the fixed

[8] The range of wavelengths transmitted by the exit pupil of the monochromator varies from about 5 mμ at 400 mμ to 45 mμ at 700 mμ.

polaroid Y_2. By turning a second knob which controls the X_4 polaroid, the percentage of the 436 mμ component in the match is varied in a manner that is compensatory to an increase or decrease in the combined amount of the 680 and 530 mμ components.

The quarter wave plate Y_0 circularly polarizes the light which is incident upon the rotating polaroids X_6 and X_2.

The quarter wave plate X_8 (rotating with the polaroid X_4) intercepts the 680 mμ and 530 mμ beams, but not the 436 mμ beam, and circularly polarizes the light so that the fraction lost by reflection at the faces of the prisms H_6 and H_8 (Fig. 4) does not vary as the polaroid controlling these beams rotates.

B. The Luminance Controls of the Test Stimulus and its Components

The test stimulus presented to the left eye may be provided by reflector R_1 (from any part of the visible spectrum), the source A_7 (680 mμ), the source A_5 (436 or 405 mμ), or a combination of either two of them (Fig. 4). When two components are used, the luminance of the stimulus is automatically retained at a relatively constant level while the proportions of the components are varied by the observer. The maximum luminance of each of the test components is set by means of the neutral wedges G_3, G_7 and G_5, respectively, to equal a given value. They therefore equal each other when their respective percentages are set at 100.

Variation in the relative percentages of the stimulus components is accomplished by means of the entrance slit F_1, the polaroids Y_7 and X_7, and the polaroids Y_5 and X_5, for the respective beams. The "Y" polaroids are fixed and the "X" polaroids rotate.

The requirements for automatically retaining the luminance of the test stimulus constant are approximated by interconnections between the slit and the polaroids. Thus, a single knob turns through 180° to change the width of the slit opening from zero to 1 mm and concomitantly rotates the polaroids for a given beam so that when the slit is opening the transmission of the polaroids is decreasing.

It is also possible to use a combination of the beams from A_5 and A_7. The beam entering the entrance slit F_1 is occluded and the polaroid Y_5 is rotated 90° so that the beam from A_5 increases as the beam from A_7 decreases. This arrangement therefore provides automatic control over the total luminance of the stimulus.

CALIBRATION OF THE APPARATUS

A. Wavelength Calibration of the Colorimeter

As described above, the reflector units of the colorimeter swing around vertical axes through the points P_3 and P_4. A pointer on each reflector indicates on a scale the wavelength of the rays from the center of its entrance slit that pass through the center of the corresponding exit pupil.

The following technique was used to calibrate these scales: The lens and prism at each exit pupil of the colorimeter were removed. By means of an achromatic erector lens, an image of the exit pupil of the colorimeter was focused in the plane of the narrow entrance slit of a spectrometer which had previously been standardized against a sodium line. This image was centered upon the slit and the spectrometer was set to read a given wavelength. The reflector of the colorimeter was adjusted to make the narrow band seen through the spectrometer eye-piece appear centered on the crosshairs. The position of the reflector was

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then marked on the scale and the whole procedure was repeated for a series of wavelengths covering the visible range.

The angular dispersion ($d\lambda/d\theta$) of the prisms H_1, H_3, H_5 and H_7 was then determined from the wavelength scale for the R_1 reflector. The widths of the spectral bands (W) passing through the exit pupil for various positions of the reflector were computed from the following equation:

$$W=(d\lambda/d\theta)\ (w_1/f_1+w_3/f_7)$$

where w_1 is the width of the entrance slit F_1, w_3 is the width of the exit pupil F_3, and f_1 and f_7 are the focal lengths of the lenses W_1 and W_7, respectively. Inasmuch as the two sides of the colorimeter are symmetrical, the resulting values also apply to the beams provided by the R_2 and R_4 reflectors on the other side of the colorimeter.

The widths of the spectral bands for various settings of the reflector are shown in Fig. 7.

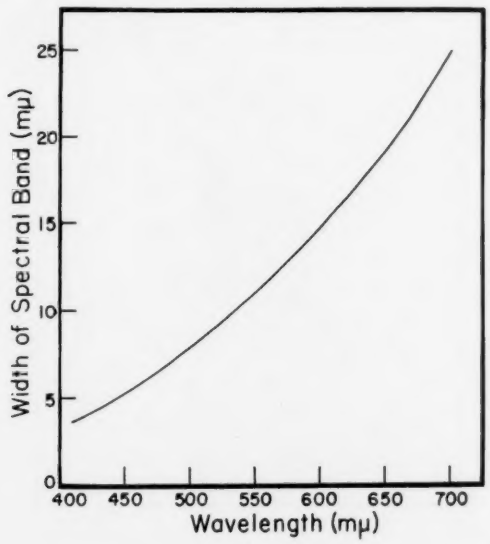

FIG. 7. The range of wavelengths transmitted by the exit pupils F_3 and F_6 of the optical system.

These widths are those obtained when the entrance slit is 1 mm and the exit pupil 0·7 mm. These bands become narrower when the width of the entrance slit is reduced to lower the luminance.

The ribbon filament source A_7 was positioned to give a 680 mμ stimulus centered on the crosshairs of the spectrometer. The width of this band is 62·8 mμ.

The A_5 mercury vapor source and the F_5 slit were positioned to center the desired spectral line (436 mμ or 405 mμ) in the exit pupil for the left eye. Similarly the A_4 mercury vapor source and the F_4 slit were positioned to center the 436 mμ line in the exit pupil for the right eye. The slits F_4 and F_5 were adjusted in width so as to make these lines just fill the exit pupils.

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B. Wavelength Calibrations of the Monochromator

The dispersing prism of the monochromator (C_9, Fig. 6) is mounted on a table which rotates around a vertical axis. A spring holds one edge of the table against the end of a micrometer screw which is calibrated to read in hundredths of a millimeter. Using the spectrometer in the manner described in the preceding section, the wavelength transmitted through the center of the F_3 exit pupil was determined for various settings of the micrometer screw. The computed widths of the spectral bands provided by the monochromator are given in Fig. 8.

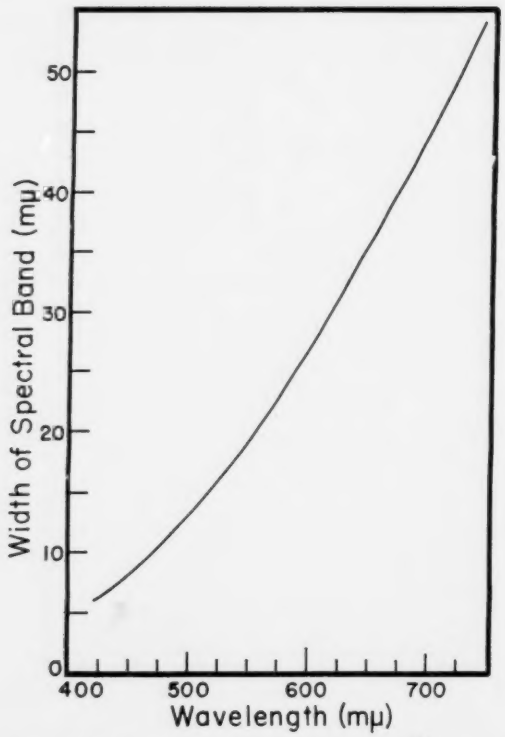

FIG. 8. The range of wavelengths transmitted by the exit pupil (F_3) for the different positions of the Pellin–Broca prism of the monochromator.

LUMINANCE CALIBRATION OF THE COLORIMETER

Both visual and electronic techniques were used for making the luminance measurements. All measurements were made with the luminance control elements intact within the instrument in order to include the peculiarities of the optical system.

As described above, the maximum values of luminance of the various stimulus components on each side of the colorimeter are made equal by varying neutral density wedges. Polaroids act as compensatory devices in automatically retaining the luminance of the composite stimulus at a relatively constant level while the proportions of the components vary. The detailed procedures used in calibrating the apparatus will now be described.

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A. Luminance Calibration of the Matching Components

The 530 and 436 mμ components of the matching stimulus were occluded so that only the 680 mμ beam passed through the V_2 stimulus target to the right eye of the observer. The polaroids for this beam were set for peak transmittance and the maximum luminance was arbitrarily set for a desired working level by rotating the G_6 neutral density wedge which was then locked in position.

The occluder was then removed from the 530 mμ beam so that two components comprised the matching stimulus. The polaroids for each of these components were set for 50 per cent transmittance and the luminance of the two beams was equated by varying the G_2 wedge for the 530 mμ beam. A sectored disc alternately occluded the two beams at a frequency required to make the luminance flicker disappear when the two beams were of the same luminance.

The 680 mμ beam was then occluded and the luminance of the standard source (A_{10}) was varied to make it equal to the 530 mμ beam by a monocular direct comparison match. The 436 mμ beam was then substituted for the 530 mμ beam and equated to the standard source by varying its neutral density wedge. The maximum luminance of each of the three matching components was therefore set equal to the same value when the polaroids controlling these components were set for peak transmittance.

The luminance level was determined with a MacBeth Illuminometer by using a slit type aperture stop and a lens mounted over the front end of the illuminometer. An image of the aperture stop of the illuminometer was focused inside the exit pupil of the colorimeter. This measurement was made with the three components of the matching stimulus adjusted to give a white approximating that of the standard field of the illuminometer.

The luminance measured in this way and expressed in cd/m^2 must be multiplied by the area of the exit pupil (1·37 mm^2) to obtain the retinal illuminance in trolands.

B. Luminance Calibration of the Test Components

The test stimuli (422 to 752 mμ) obtained with the reflector (R_1) were equated in luminance (27 cd/m^2) to the matching stimulus by means of a monocular direct comparison match on appropriate dichromatic mixtures. The luminance of the A_4 and A_7 auxiliary sources was equated to monochromatic components of the matching stimulus in the same manner. These measurements were made with the monocular viewing device shown in Fig. 6.

The visual comparisons between the three matching primaries (436, 530 and 680 mμ) and corresponding wavelengths from the test spectrum were subsequently checked by more precise electronic methods. Averages from five readings on the electronic comparisons fell within 3·5 per cent of those obtained visually. The instrumentation and procedures used for these measurements are discussed in the following section.

C. Transmittance of Wedges, Polaroids and the Variable Slit

The Beckman DU Spectrophotometer (with photo-multiplier attachment) was used to measure the transmittances of the luminance control elements intact within the apparatus. This was viewed as desirable due to the complexity of the optical system. These measurements were obtained in the following manner.

The phototube housing was removed from the spectrophotometer and carefully positioned in front of the monocular viewing apparatus (Fig. 6) which was attached to the front of the colorimeter. The beams from the exit pupils of the colorimeter F_3 and F_6 were both

brought to a focus at the center of the aperture F and were then transmitted through a piece of ground glass mounted over the window of the phototube housing. The "blue" phototube was then adjusted laterally by small amounts until it produced a maximum response as indicated by lateral deflections on the milliammeter of the spectrophotometer. This adjustment was the same for each of the two beams, but only one beam was used at a time.

The procedure for using the instrument under these conditions deviated from the company specified techniques (BECKMAN, 1958) only in that monochromatic beams from the colorimeter were used to operate the instrument instead of the source provided with it. Thus, the spectrometer was first nulled for the reference standard level and again at each of

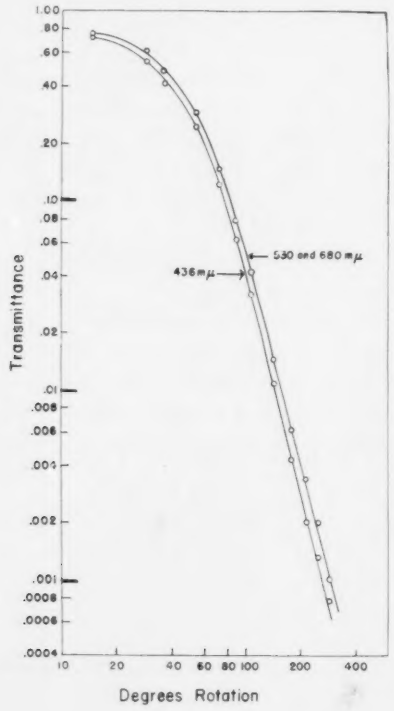

FIG. 9. Transmittance of the neutral density wedge G_8 (Fig. 5) as a function of degrees rotation from an open sector.

the selected positions of increased wedge density. Periodic checks were made on the reference standard (which was always maximum transmittance of the wedge) for different beam intensities with the sensitivity of the instrument held constant, and also with the converse arrangement. Its variation was never more than 2 per cent and at medium sensitivity levels it held within 0·5 per cent.

Transmittance measurements on the G_8 neutral density wedge are presented in Fig. 9 as a function of degrees rotation from an arbitrary starting point which corresponds to the center of an open sector having a transmittance of 1·0. Both ordinate and abscissa values have been plotted on a log scale, as this gives a linear plot throughout nearly two log units.

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The data for 530 and 680 mμ were nearly identical and were averaged, plotted and fitted with a single curve in Fig. 9. The data for 436 mμ differ from that for 530 and 680 mμ enough to justify a separate curve. However, the vertical separation between the two curves is constant enough to assume that the ratio of the three wavelengths remains unchanged when the wedge position is varied.

The arrangement of the Beckman Spectrophotometer just described permitted convenient determination of the transmittances of the various polaroids and the F_1 variable slit with these elements intact within the apparatus. Measured deviations from the theoretical values provided the information required for making appropriate corrections in the data.

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THE EFFECTIVE PUPILLARY AREA AT VARYING PERIMETRIC ANGLES

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Abstract—The effective pupillary area was measured at varying perimetric angles by photographing the fundus glow. The present results are smaller than those of previous investigations because the iris edge was excluded from the estimate of pupil size.

Résumé—L'aire pupillaire effective est mesurée en fonction de l'angle périmétrique en photographiant la lumière réfléchie du fond d'oeil. Les résultats obtenus sont plus faibles que ceux des travaux antérieurs parce que le bord de l'iris est exclu de l'estimation de l'aire pupillaire.

Zusammenfassung—Die effektive Pupillengrösse wurde für verschiedene Einfallswinkel gemessen, indem das vom Fundus reflektierte Licht fotografiert wurde. Die Ergebnisse der gegenwärtigen Messungen liegen niedriger als frühere Angaben, weil der Irisrand von der Einschätzung der Pupillengrösse ausgeschlossen war.

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IN problems of visual physiology, and in quantitative perimetry, where the amount of light reaching the retina per unit time needs to be known, a knowledge of the pupillary area is important. This is because, as stated by DUBOIS-POULSEN (1952), the illumination of the retinal image is a function of three variables, the luminance of the test-object, the transmission of the ocular media, and the area of the pupil. At first sight it would appear that photography of the pupil offers a simple method of estimating its area, though difficulties may be encountered which affect the accuracy of this method. As the area of the pupillary aperture decreases rapidly at large angles of view, accurate fixation by the subject is important, and because of the small depth of focus of much of the photographic apparatus used, focussing is critical. WAITE, DERBY and KIRK (1925) criticized photographic methods of estimating pupillary size because the iris pigment epithelium often extends on to the anterior surface of the iris so increasing its apparent size, and WEALE (1956) observed that iris thickness reduces the apparent pupillary area at larger angles of view, again because the iris pigment epithelium is difficult to distinguish from the edge of the pupil. SPRING and STILES (1948) and SLOAN (1950) measured the pupillary area at various angles of view, but did not consider the thickness of the iris. The effect of this and related factors is considered in the following pages which contain a description of measurements made on both dilated and natural pupils by a method which excludes the iris pigment epithelium from having any effect on the results.

METHOD

The eye was illuminated along the axis of view so that the fundus glow produced could be photographed against a dark iris in such a way as to give a true record of the effective pupil. The apparatus used was an A.I.M. slit-lamp modified in the following manner: the

binocular microscope was removed and a 35 mm Asahi Pentax single-lens reflex camera clamped to the microscope arm; the mirror was removed from the lamp column and a glass slide, angled at 45° about a horizontal axis, attached to a collar made to fit the top of the lamp column. The camera had a 25 mm extension tube fitted between a 55 mm *f*2 lens and its body, and could be swung through 200° in the horizontal plane on the arm to which it was attached. Ilford F.P.3 film was used, the exposures being $\frac{1}{15}$ sec at *f*2, and the film was developed in Promicrol according to the manufacturer's instructions. For the dilated pupil experiments the right pupil was dilated with 2 per cent homatropine and 10 per cent phenylephrine drops, repeated half-hourly until the pupil showed no further reaction to light. The subject fixated on a $1\frac{1}{2}$ mm black target on a white background at a distance of 120 cm (subtending at the eye an angle of 4′), and the angle between fixation and camera was measured with a protractor attached to the slit-lamp table. For the natural pupil experiments the pupil was allowed to remain freely mobile and a control camera was placed at 30°

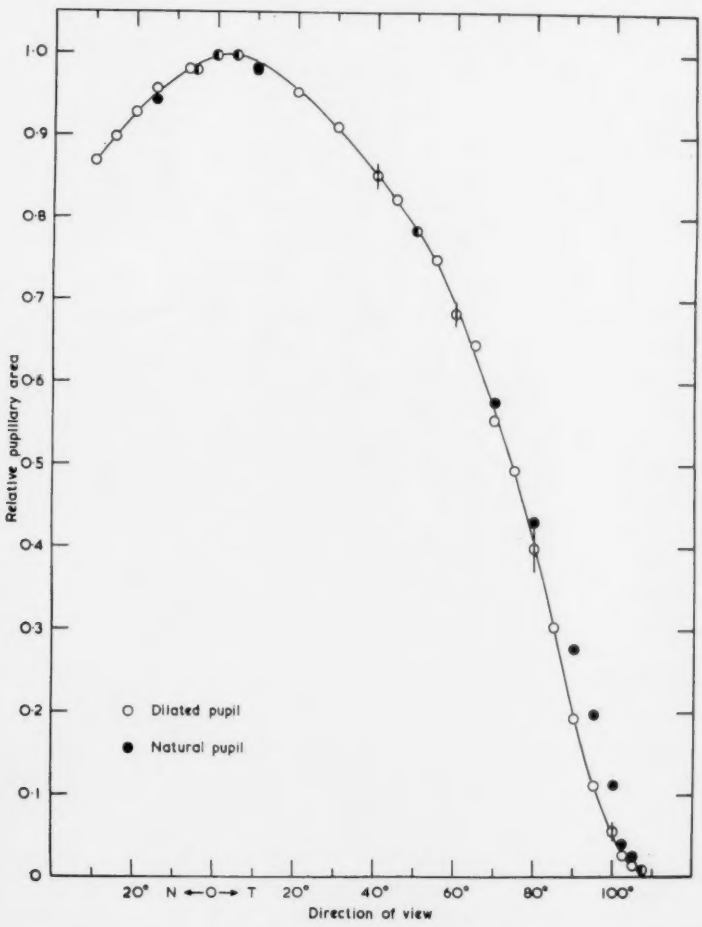

FIG. 1. The relation between relative pupillary area and direction of view for dilated and natural pupils.

on the temporal side of fixation. This was an Edixa 35 mm single-lens reflex camera, with a 135 mm *f*3·5 lens and a 60 mm extension tube. For technical reasons Ilford H.P.3 film was used in the control camera, the exposures were $\frac{1}{10}$ sec at *f*3·5 and the film was developed in Promicrol. Both cameras were triggered simultaneously so that the effective pupillary areas could be compared with each other.

The developed negatives were projected at a linear magnification of ×20 on to millimetre graph paper, the horizontal and vertical diameters of the pupil were measured and the area of the pupil estimated by counting the squares covered by the black fundus glow image. Although the control images were photographed by anterior illumination and not by the fundus glow method, any error that might occur because of this was negligible as the iris thickness is without appreciable effect on pupil area at eccentricities less than about 70°.

Eight subjects were used in these experiments, three male and five female, their ages ranging from eighteen to thirty-eight years.

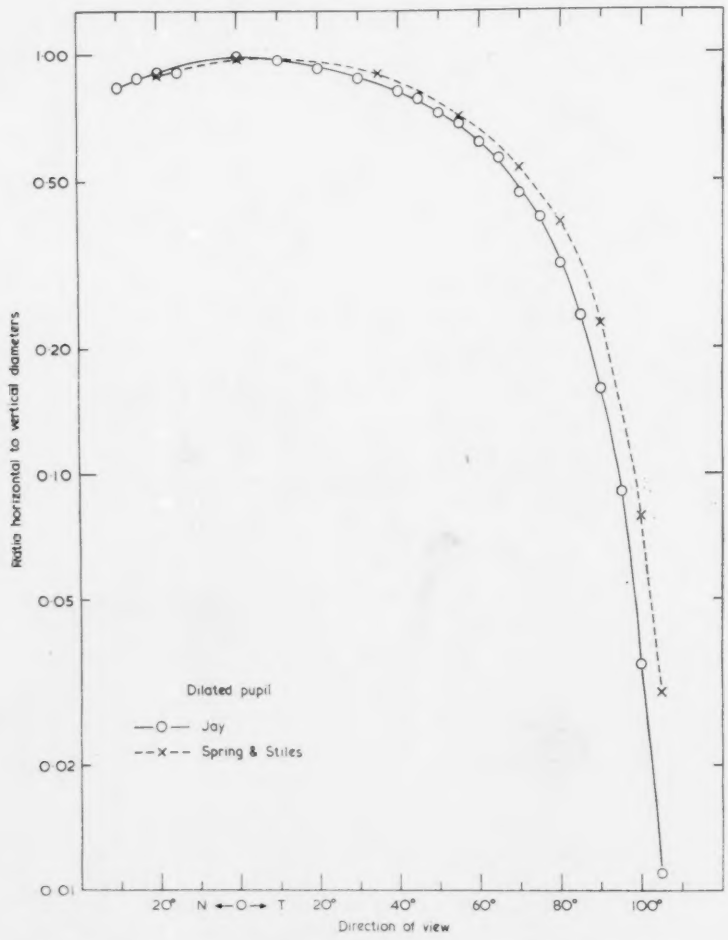

FIG. 2. The ratio of horizontal to vertical diameters of the dilated pupil with varying direction of view.

RESULTS

(1) *Dilated Pupil Experiments*

The areas of the pupil at varying perimetric angles were plotted for each subject so that the angle at which the effective pupillary area was maximal could be determined. This angle varied from subject to subject; its mean value being 3° on the temporal side. The maximum ordinates for each subject were equated, and the averages of the relative areas for each angle of view plotted in Fig. 1 and tabulated in column 2 of the table. The standard errors of the means were calculated for arbitrarily chosen values and are shown in Fig. 1. The mean ratios of horizontal to vertical diameters are tabulated in column 3 of the table and are plotted in Fig. 2 where they are compared with those of SPRING and STILES (1948).

(2) *Natural Pupil Experiments*

The calculations are similar to those for the dilated pupil experiments except that the

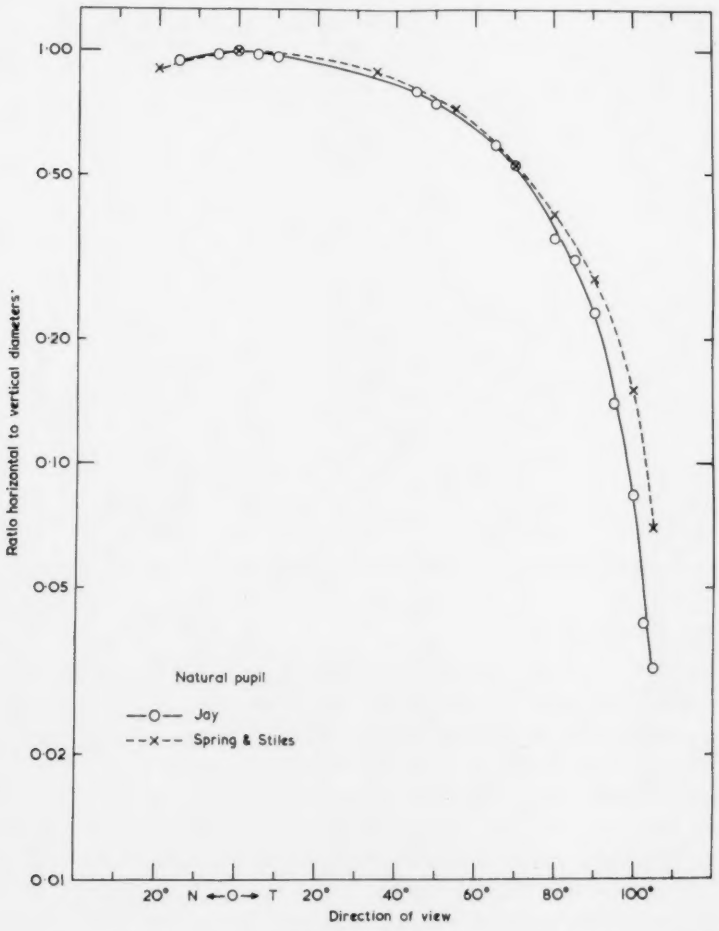

FIG. 3. The ratio of horizontal to vertical diameters of the natural pupil with varying direction of view.

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areas were calculated from the area of fundus glow image divided by the control pupillary area, and the horizontal to vertical ratios calculated in a similar manner. The mean relative areas are plotted in Fig. 1 where they can be compared with those of the dilated pupils and are tabulated in column 4 of the table. The mean ratios of horizontal to vertical diameters are tabulated in column 5 of the table and are plotted in Fig. 3 where they can be compared with those of SPRING and STILES (1948).

TABLE 1

Direction of view	Dilated pupil		Natural pupil	
	Relative area	Ratio of hor./vert. diam.	Relative area	Ratio of hor./vert. diam.
30°	0·869	0·84		
25°	0·898	0·88		
20° ↑	0·927	0·91		
15° |	0·957	0·93	0·943	0·95
5° N.	0·980	0·98	0·979	0·98
0°	0·997	0·99	0·997	1·00
5° T.	0·997	0·99	0·996	0·98
10° |	0·983	0·97	0·981	0·97
20° ↓	0·952	0·93		
30°	0·910	0·88		
40°	0·851	0·82		
45°	0·822	0·79		
50°	0·784	0·73	0·784	0·75
55°	0·749	0·69		
60°	0·682	0·62		
65°	0·645	0·57		
70°	0·553	0·47	0·575	0·53
75°	0·493	0·41		
80°	0·398	0·32	0·431	0·35
85°	0·303	0·24		
90°	0·192	0·16	0·277	0·23
95°	0·111	0·091	0·197	0·14
100°	0·055	0·035	0·113	0·084
102·5°	0·026	0·020	0·040	0·041
105°	0·013	0·011	0·025	0·032
107·5°	0·008	0·004	0·008	0·007

DISCUSSION

(1) *Dilated Pupil Experiments*

SPRING and STILES (1948) apparently calculated their pupillary areas by assuming these areas to be elliptical in shape. As this assumption is only valid up to eccentricities of about 70° their pupillary areas are not compared with those of the present experiments. On comparing the ratios of horizontal to vertical diameters in Fig. 2, it will be seen that the present results are consistently smaller than those of the above authors at angles of view of 70° and over. This difference is probably due to the iris pigment epithelium increasing the apparent size of the pupil in the results of those authors. An attempt was made to calculate this effect of iris thickness; the difference between the two sets of results is compatible with an iris pigment epithelium edge of 0·3 mm with an 8 mm pupil and a corneal radius of curvature of 7·8 mm in its central part, flattening out towards the periphery in accordance with the data of GULLSTRAND (1911). At very large angles of view there were difficulties

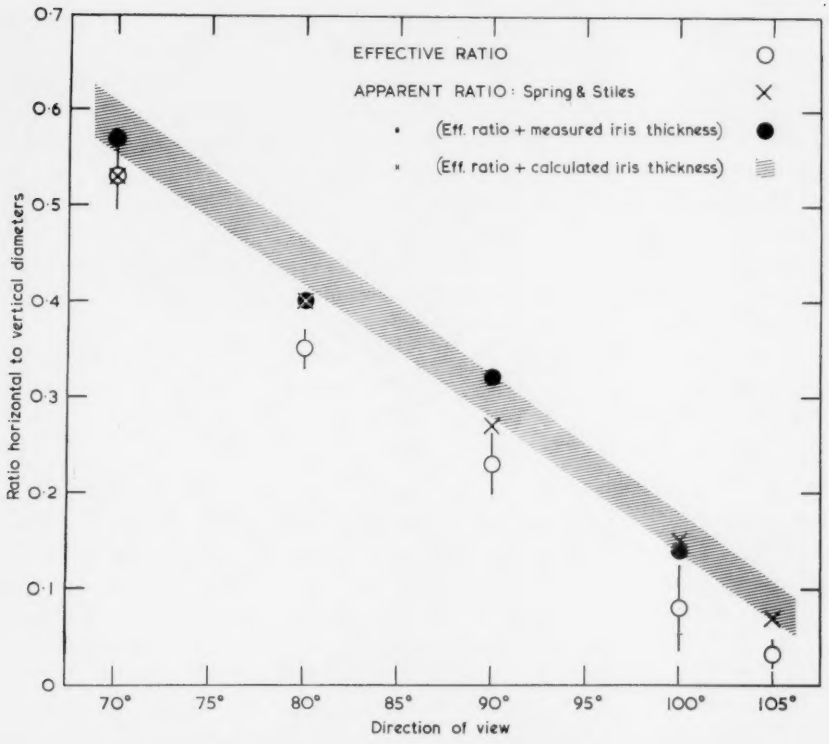

FIG. 4. A comparison between the ratios of horizontal to vertical diameters for the effective pupil and for the apparent pupil (both measured and calculated) at large eccentricities.

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in measuring the area of fundus glow image. These difficulties were due to the light scatter in the cornea as a result of the total internal reflection that occurs particularly at large angles, and also to the small depth of focus of the apparatus used. These effects caused blurring of the image which tended to increase its apparent size. At angles of view of over 100° the average results were probably also less accurate because a fundus glow could not be observed in every subject.

(2) *Natural Pupil Experiments*

Fig. 3 shows that the present results are consistently smaller than those of SPRING and STILES (1948) at angles of view of over 70°; but the difference is less marked than in the dilated pupil experiments because the iris is thinner with a small pupil and the iris edge correspondingly less obvious. In order to test the hypothesis that the difference between the present results and those of SPRING and STILES (1948) is due to the iris pigment edge, this edge was both photographed on colour film (Kodak High Speed Ektachrome) and calculated. Let the ratio of horizontal to vertical diameter in the natural pupil experiments be D_H/D_V. Then if the hypothesis is correct the small pupil results of SPRING and STILES (1948) may be stated as D_H+T/D_V where T is the apparent thickness of the iris edge. The colour film measurements of the iris edge (T_P) were made at four eccentricities between 70° and 100° and

the ratio D_H+T_P/D_V plotted in Fig. 4 and compared with the present results and with those of SPRING and STILES (1948). The apparent thicknesses (T_C) of irides with 0·1, 0·2 and 0·3 mm actual edge thickness were then calculated at these angles of view by tracing rays from the iris edge through a cornea with peripheral flattening as described above. The range of D_H+T_C/D_V is indicated in Fig. 4 by the cross-hatching. The difference between the present results and those of SPRING and STILES (1948) is seen to be consistent with an effective iris pigment edge of between 0·1 and 0·2 mm thick, a value confirmed in an examination of a number of histological sections of iris.

The difference between the large and small pupil relative area curves in Fig. 1 is accounted for by the flattening of the peripheral cornea which lessens the apparent size of the dilated pupil to a greater extent than that of the small pupil.

SLOAN's (1950) results for a large pupil are also greater than the present ones, but Sloan only examined one subject and there is considerable individual variation in pupil area at varying angles, so no comparison has been made between her results and the present ones.

CONCLUSIONS

In any problem where a knowledge of the amount of light reaching the retina is required, an accurate estimation of the area of the pupil is essential. When the retinal image is within 30° of fixation the error that occurs by ignoring the thickness of the iris edge is minimal, but at larger angles of view this edge decreases the pupillary aperture to an increasing extent. At 80° the difference is nearly 10 per cent, at 90° 20 per cent and at 100° over 40 per cent, so in problems concerning the response of the more peripheral parts of the retina any method of estimating the area of the pupil must exclude the iris edge. Another factor that has to be considered is the wide variation in pupillary area from subject to subject at any one angle of view, therefore this area should be measured in the subject under test whenever possible.

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ACCOMMODATION AND CONVERGENCE IN THE ABSENCE OF RETINAL IMAGES

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Abstract—The behaviour of accommodation and convergence of the eyes in total darkness and in very low illumination has been studied by an objective method. Also the ability of subjects to accommodate and converge to the position of their own finger held up in darkness has been recorded. Simultaneous records show that both accommodation and convergence are active in darkness, but fluctuate without relation to one another. Results also show that the brain is unable to use the information from proprioceptor nerves of the hand and arm to direct the eyes and control accommodation in darkness. The synergic relation between the innervations to accommodation and convergence still holds near the threshold, although the accommodation activity of night myopia is present, but when there is no retinal image the two mechanisms act independently.

Résumé—On a étudié par une méthode objective le comportement de l'accommodation et de la convergence des yeux dans l'obscurité totale et pour un éclairement très faible. On a enregistré aussi l'aptitude des sujets d'accommoder, et de converger sur la position de leur propre doigt tenu vertical dans l'obscurité. Les enregistrements simultanés montrent que l'accommodation et la convergence sont actives toutes deux dans l'obscurité, mais que leurs fluctuations sont indépendantes. Les résultats montrent aussi que le cerveau est incapable d'utiliser l'information des nerfs proprioceptifs de la main et du bras pour diriger les yeux et contrôler l'accommodation dans l'obscurité. La synergie entre les innervations de l'accommodation et de la convergence subsiste encore près du seuil, malgré la présence de la myopie nocturne dans l'accommodation, mais quand il n'y a pas d'image rétinienne les deux mécanismes fonctionnent indépendamment.

Zusammenfassung—Es wurden Akkommodation und Konvergenz der Augen bei absoluter Dunkelheit und bei sehr geringer Beleuchtung mit einer objektiven Methode untersucht. Es wurde auch untersucht, ob Personen bei Dunkelheit auf ihre vorgehaltenen Finger akkommodieren und konvergieren können. Gleichzeitige Untersuchungen haben gezeigt, dass Akkommodation und Konvergenz bei Dunkelheit wirksam sind; sie wechseln jedoch ohne Beziehung zueinander. Die Ergebnisse zeigen, dass das Gehirn nicht in der Lage ist, bei Dunkelheit die Information der proprioreceptiven Nerven der Hand und des Armes zur Lenkung der Augen und Steuerung der Akkommodation zu verwenden. Die synergistische Beziehung zwischen den Innervationen von Akkommodation und Konvergenz liegen immer nahe einer Schwelle, obgleich die Akkommodationsaktivität bei der Nachtmyopie vorhanden ist. Ohne Netzhautbilder wirken die beiden Mechanismen jedoch unabhängig voneinander.

INTRODUCTION

IT is a commonly held opinion that accommodation and convergence are, to a great extent, under the control of the will. Another view is, that while one of these functions is voluntary, the other reacts with it by reflex. The existence of this reflex is clear in the case of accom-

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modation. It appears to be controlled by the convergence of the eyes, and to a less extent by the vergence of the light striking the retina (FINCHAM and WALTON, 1957). These two controls ensure that in normal vision the amount of accommodation in dioptres is approximately equal to the convergence measured in metre-angles, i.e. the eyes focus upon the point to which the visual axes converge. Another reflex which should be mentioned in this connexion is fusion. It acts as a fine adjustment to convergence in the same way as the light-vergence reflex acts to accommodation. Accommodative-convergence, which is demonstrated during monocular fixation of a near object, is generally thought to be a reflex reaction of convergence to accommodation, but it may be evidence of the convergence effort which is called into play to induce the necessary amount of accommodation.

It is not intended in this paper to discuss the relation of accommodation to convergence, but sufficient has been said to support the view that these two functions are under synergic control. Also it will be seen that irrespective of voluntary control, the precise adjustment of both accommodation and convergence must depend upon the presence of discrete retinal images to stimulate fusion, and having the necessary optical properties to control accommodation.

The work described in this paper was done with two objectives: to study how far accommodation and convergence can be controlled by the will in the absence of retinal images, and to test whether the synergic link between these faculties is a reflex, dependent for its initiation on retinal stimulation. It is well known that in darkness and in very low illumination, accommodation occurs—a phenomenon usually called night myopia. A similar activity of accommodation occurs when the retinae receive general illumination without discrete images on which the eyes may be focused. Although few of the workers who describe experiments on this subject have stated whether an effort was made to adjust the eyes for distance, we may assume this to be the case. The earliest investigators had noticed that at night it was necessary to adjust viewing instruments, such as binoculars, to give divergent light. Likewise empty-field myopia, investigated by WHITESIDE (1952) and by CAMPBELL and WHITESIDE (1953), was probably first reported by airmen who were trying to see distant aircraft in a uniform sky. Therefore, under these conditions accommodation was not being controlled by the will.

It has also been shown by CAMPBELL (1953) and by WESTHEIMER (1957) that the accommodation which occurs in the absence of retinal images shows relatively large fluctuations with a random frequency. Some preliminary experiments by the author showed that convergence was also active in darkness and the amount varied from time to time with a given subject. If these differences were caused by fluctuations in unison with those occurring in accommodation, it would appear that the synergic link between the two functions was firmly established and not conditioned by the requirements of vision. IVANOFF (1956) and IVANOFF and BOURDY (1954) found by a subjective method that the eyes converged during monocular fixation of a very weak visual stimulus. Because this convergence was comparable with the accommodation found under the same conditions on a previous occasion, it was concluded that the synergy between accommodation and convergence still existed in the conditions of night myopia. In view of the random fluctuations that have been found, we can only test whether the linkage exists in darkness by recording accommodation and convergence at the same instant. The present paper is a description of this test made on a number of subjects by an objective method. The same method has been used to record simultaneous accommodation and convergence during fixation of an object in very low illumination.

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It is understandable that the adjustment of the eyes for the somewhat indefinite position of optical infinity without some guidance may present a mental difficulty, and therefore the following experiment was also made. The state of accommodation and convergence was recorded while the subject attempted to look to the position of his finger held at $\frac{1}{3}$ m in darkness. The results of this experiment are an estimate of the ability of the brain to use the information it has of the position of the finger to direct the eyes and control accommodation.

METHOD

Measurement of Convergence

The radius of curvature of the cornea is approximately 8 mm so that the surface acts as a convex mirror of 4 mm focal length. If the light from an illuminated aperture is projected on to the cornea by an optical system similar to a slit-lamp, and is focused towards a point 3·9 mm behind the surface, the light will be reflected to form an image at 180 mm in front of the cornea. This image will be magnified to 46 times the size of original projected image. The locus of the axes of rotation of the eye lies about 5 mm behind the centre of curvature of the cornea, and therefore, as the eye rotates, an image reflected from the cornea will be moved in the direction opposite to the movement of the visual axis. Because of the magnifi-

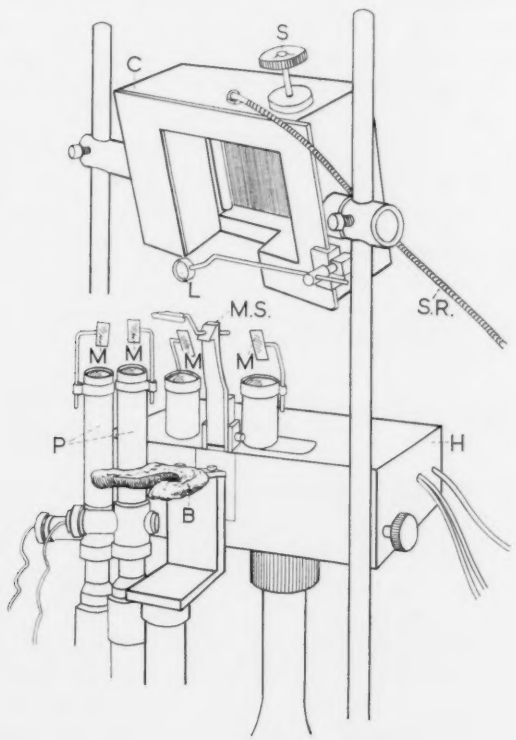

FIG. 1. Illuminating apparatus and camera: H, housing for lamps and optical system for producing slit images from cornea; P, illuminating systems for Purkinje images; M, mirrors; C, camera; S, shutter setting mechanism; S.R., shutter release; L, lens for photographing Purkinje images; M.S., lever of micro-switch; B, wax dental impression.

cation in the system just described, small rotations of the eye will cause appreciable movement of the image received on a screen or photographic material; for a subject whose inter-pupillary distance is 65 mm, convergence from the parallel position to a point at 1 metre (1 metre-angle) causes the image on the screen to be moved 12 mm, the other eye remaining fixed. The amount of this movement will of course vary with inter-pupillary distance and radius of curvature of the cornea.

In order to measure changes in convergence it is necessary to receive an image from each eye. Therefore two projection systems were provided, each forming a fine vertical line image just behind the corneal surface. The required position of these images was arrived at by racking the apparatus forward or backward relative to the eyes until sharp line images from the corneae were received on the focusing screen of a camera. The separation of the two projection systems was adjustable to accommodate for variations in inter-pupillary distance. As it was necessary to allow the subject a clear view of certain fixation marks placed beyond the apparatus, the light from the two projection systems was directed upward and reflected by small mirrors on to the eyes at an angle of about 30° with the visual axes, which were horizontal. The camera receiving the images could thus be placed above the visual axes, so that the subject's fixation was not obstructed. The general arrangement is shown in Fig. 1.

The illumination of the systems was produced by either a tungsten lamp for adjusting the apparatus or a small electronic flash tube for recording. The flash tube and the tungsten lamp were mounted on each side of a right-angle reflecting prism which could be rotated through 90° so that light from either source could be reflected through a condensing lens and a slit. Only one slit was used for the two projectors; by means of reflecting prisms the light from half the slit was directed into one projector and half into the other.

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Measurement of Accommodation

Accommodation was measured by the familiar method of recording the size of images reflected from the anterior surface of the crystalline lens (3rd Purkinje image). The illumination for these images was provided by two small projection systems which were vertical and had surface-silvered mirrors above the projection lenses to reflect the light on to the left eye. These systems also had alternative light sources: tungsten for adjustment and electronic flash for photography. The tungsten lamps were mounted on slides which allowed them to be removed and exactly replaced by a small aperture. A condensing lens mounted below this, focused light from the flash tube on to the aperture.

The simultaneous reception of the corneal images from the two eyes and the reflections formed at the anterior surface of the lens of the left eye on one photographic plate presented some difficulty. The corneae were made to form real images, i.e. the images were received directly on the plate without an intervening lens. The crystalline lens images on the other hand are virtual; the light diverges as from a position about 8 mm behind the plane of the pupil. To record these a photographic lens must be used, but it must be so placed that it neither receives light from the line images from the cornea, which would obliterate the lens images, nor masks the reception of the corneal images in various positions on the plate. A single achromatic lens of 35 mm focal length and 5 mm diam. was used.

The illumination of the eye for the images from the lens surface must also cause strong reflections from the corneal surface. These corneal reflections were of course imaged by the photographic lens, but some light missed the lens and fell directly on the plate causing

fogging. This objection was reduced to a great extent by using very oblique illumination and photographing from such a position that the lens images were seen at their maximum brightness and central in the pupil while the full light reflected from the cornea was avoided. It was also arranged that only a very small part of the eye was illuminated, thus the iris, sclera and surrounding parts which would scatter light were dark and do not appear in the records.

The camera consisted of the back of a $3\frac{1}{2} \times 2\frac{1}{2}$ in focal-plane camera, i.e. shutter and carrier for ground glass screen and dark slides. The lens for photographing the Purkinje images was attached to this and mounted out in front on a fine rod with provision for centring and focusing. The camera was fixed to the illuminating system and the whole apparatus mounted on a heavy stand, with forward and backward and transverse drives.

The subject's head was held by means of a wax dental impression, which in the initial adjustments could be swung to rotate the head until the line images from both eyes were in focus on the screen. When this position was reached, the bite was fixed and two pads were brought to bear on the temples. Before records were made, two other rests were placed against the back of the head. Small changes in the distance between the apparatus and the eyes, occurring during an experiment, would have affected not only focus but also the position of the line images from the corneae, and so would have given false results. This was prevented by fixing on the apparatus a very sensitive micro-switch with an operating lever made to bear on the bridge of the subject's nose. This switch was connected to a relay which completed the circuit of the electronic flash tubes. During the initial adjustments of the apparatus the pressure on the micro-switch could be released. When correct focus of the images was obtained the pressure was adjusted to operate the flashes, and the whole apparatus was then racked away from the subject. To make the exposures the camera shutter was opened and the apparatus racked forward until the pressure of the lever of the switch on the subject's nose caused the relay to fire the flashes.

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Visual Fixation and Calibration of Results

In these experiments it was necessary that one eye, the left, should remain approximately fixed, and that movements of vergence should be confined to the right eye. This was in order to be sure that the line images from the corneae were received in suitable positions on the plate and also that the direction of illumination for the lens images, and hence their position in the pupil, did not change. This fixation was governed by presenting to the left eye a ring of eight faint blue spots of light. This light was convergent 1·5 dioptres at the eye and so did not stimulate accommodation. The ring of spots had an angular diameter of 8·5°. Fixation marks which were used in the calibration records were placed so that their image for the left eye was central in the ring, and in the experiments when no fixation mark was present the subject was told to look through the centre of the ring.

To interpret the meaning of results in terms of dioptres of accommodation and metre-angles of convergence, it was necessary to make calibration curves relating the change in size of the lens images to accommodation, and the separation of the line reflections from the corneae to convergence, at each experiment. Therefore in addition to the condition which was being tested records were taken with the subject fixating a distant object, one at 1 m and one at $\frac{1}{2}$ m, or $\frac{1}{3}$ m. The fixation mark for the finite distances was simply a spot of red light about 3 mm diam. with a vertical black line of about 0·5 mm width across it to encourage precise fixation and accommodation. An optical system was necessary to present

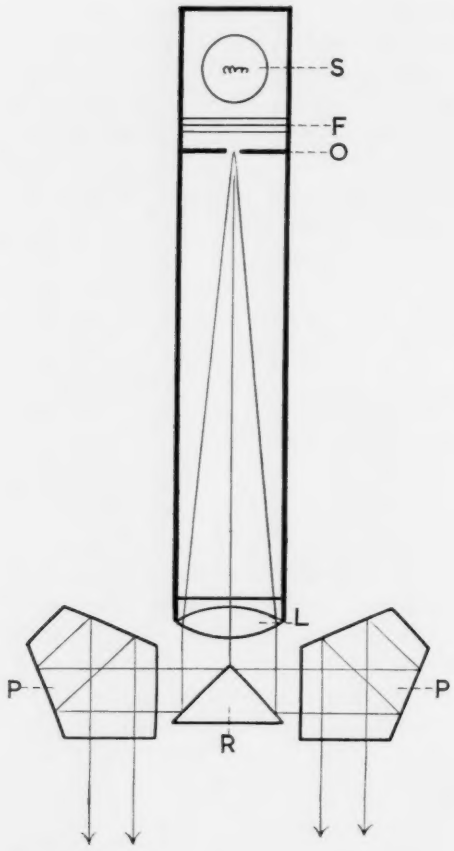

FIG. 2. Binocular collimator for distant fixation: S, tungsten lamp; F, filter and diffusing screen; O, object; L, achromatic lens; R, right-angled prism; P.P., pentagonal prisms.

a distant fixation mark binocularly. The principle of this is shown in Fig. 2. It is in effect a binocular collimator. The object, a small cross cut in an opaque disk, is placed at the principal focus of an achromatic lens. This is followed by a silvered right-angled prism from the faces of which the light is reflected into two pentagonal prisms. The result is that two beams of parallel light emerge parallel to one another and are presented to the subject's eyes. The apertures of the prisms were large enough to avoid the necessity to adjust the separation for various inter-pupillary distances. The object was coloured red by a filter with maximum transmission of 610 mμ, the luminance was approximately 1 ft-lambert.

Subjects

The ages of the subjects ranged from 18 to 32. They were all either emmetropic or slightly hypermetropic. Myopes could not be used because they would not accommodate correctly when viewing the near object used for calibration. Some selection was necessary because of the great variation which occurs in the definition of the 3rd Purkinje image, and a few subjects had to be rejected because the images were not sufficiently clear. In some

subjects there was a somewhat abnormal angle between the optical axis of the crystalline lens and the visual axis; this is associated with variation of angle alpha. It necessitated moving the lens used to photograph the Purkinje images to collect the light reflected from the centre of the crystalline lens surface. Another point should be mentioned regarding this method of measurement. It is known that in a few subjects the change in the third image is slight relative to the change in accommodation. The reason for this anomaly is not known, but it is presumed that in these cases the surfaces of the internal layers of the lens are optically more effective. The accuracy of the determination of accommodation by the method of comparing the size of the images reflected by the front surface of the lens is obviously impaired in such cases. One subject was rejected for this reason when the calibration records were examined.

Procedure

Before each experiment the subject's horizontal muscle balance was measured by the usual clinical method. While the subject viewed a fixation light at 6 m, a Maddox rod was placed before one eye, and that eye covered. The subject stated the position of the streak of light as soon as the eye was uncovered. Only subjects who gave the same results for right and left eyes were used. It will be noticed in the results (Table 1) that the muscle balance of some subjects varies from one experiment to another. Such variations are common, and may depend on fatigue at different times of the day. For this reason the muscle balance was measured before each experiment. Exophoria signifies a tendency to divergence and esophoria to convergence when fusion is prevented.

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The records of accommodation and convergence were made as follows: when the subject was in position on the bite, the room was darkened and the subject was directed to look at the image in the binocular collimator and to ensure that he was seeing it with both eyes and had single and clear vision. The image was seen in the centre of the ring of blue dots. The apparatus was then focused and centred using tungsten illumination, and the pressure of the micro-switch was adjusted to close at this position. The apparatus was then racked slightly away and the circuit changed from the tungsten lamps to the flash tubes. With the plate in position the shutter was opened and the apparatus racked forward until the pressure on the bridge of the nose caused the micro-switch to fire the flash tubes. Thus the first record was made with distant fixation. The second record was made while accommodation and convergence were unstimulated. For this the fixation mark was switched off and the subject tried to look into the distance through the centre of the ring of blue dots. This was followed by two more records: one with fixation of an object at 1 m and another with the object at $\frac{1}{2}$ m. As mentioned previously the three records made during fixation were for calibration. Between each record it was necessary to rack the apparatus away from the subject so that the power packs supplying the flash tubes could recharge, to change the dark-slide and reset the shutter, and change the fixation mark. The time taken for this was about 1 min.

To test the subject's ability to look to the position of the finger held up in darkness the following routine was used. Again four records were made, the first three, in this case, being for calibration. The first was made with the distant object, the second with the object at 1 m and the third with it at $\frac{1}{3}$ m. The subject then placed his finger on the small illuminated aperture at $\frac{1}{3}$ m and the light was switched off. He was then told to look away into the distance and then back to the position of the finger. The record was then made. In these experiments on the conditions of the eyes in total darkness, fixation objects used for calibra-

tion were aligned with the primary position of the visual axis of the left eye upon which the ring of blue dots was also centred. Thus in all the records the direction of the left visual axis should be unchanged. (N.B. This alignment was not quite achieved in the example shown (Fig. 3). The line image from the left cornea has moved.)

In determining the condition of accommodation and convergence during low illumination of the fixation mark, the usual three calibration records were made; then the collimated image was again shown, but the right pentagonal prism (Fig. 2) was covered, so that the subject had monocular fixation, left eye. A record under these conditions with full illumination of the object gave an objective measurement of horizontal muscle balance. For the record with a very low stimulus a 2·0 density filter was placed over the left prism and a neutral wedge filter introduced between the lamp and the object in the fixation apparatus (Fig. 2). This filter was adjusted to reduce the light until the subject signalled that he could only just see the object but was still sure of fixation. The record was then taken. No attempt was made to relate the luminance of the object to the subject's threshold.

The three calibration records were made to cover only the range within which it was anticipated that accommodation and convergence would vary when the subject attempted to look into the distance in darkness, i.e. from infinity to $\frac{1}{2}$ m. Extrapolation was necessary in those cases which showed divergence and in one case where convergence exceeded 2 metre-angles. The calibration graph for convergence was substantially a straight line, its slope varied with the inter-pupillary distance. Previous workers have agreed that an accuracy within $\pm 0{\cdot}2$ D can be expected from the Purkinje image method of measuring accommodation. In the example shown in Fig. 3, in which fixation was for infinity (A) and for 1 m (B), the original negatives show a difference in the separation of the convergence lines of 11·5 mm, and between the 3rd Purkinje images of 0·8 mm. Measurements were made by projecting the negatives to a magnification of about 6. It was found that the most accurate method of measuring the separation of these projected images was to place a small pencil mark in the centre of each image and to measure the distance between these.

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RESULTS

The values shown in the following tables are not measurements of absolute accommodation and convergence. They are relative to the conditions when the subjects were fixating objects at infinity, and at certain known distances. Metre-angles of convergence are comparable with dioptres of accommodation. Negative values signify divergence of the visual axes.

Most subjects said after the experiment that they were not confident they had succeeded in looking into distance. One thought that in spite of his efforts he was looking at a point less than 1 m away, but when the plates were developed it was found that at the moment of exposure his accommodation and convergence were in fact zero.

In the experiment in which subjects tried to look to the position of their finger at $\frac{1}{3}$ m, they reported again that they had no confidence of success. In one case the accommodation was correct, but any special ability that this result appears to show is discredited by a repeat result from the same subject when the accommodation was less than half the correct amount.

The results of seven experiments to show the relation of accommodation to convergence during monocular fixation of an object with very low luminance are shown in Table 3 and Fig. 8. It was necessary to use monocular fixation in this test to avoid convergence being

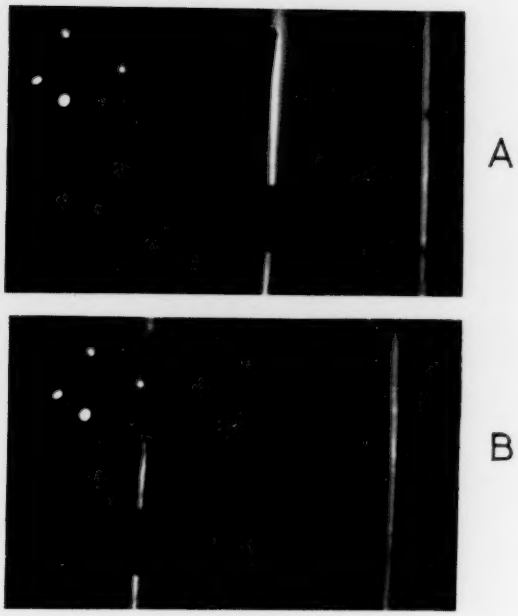

FIG. 3. Simultaneous records of convergence and accommodation: (A) subject fixating distant object; (B) subject fixating object at 1 m. The line images are reflected from the corneae, their separation gives the measure of convergence. The upper pair of dot images in each case is reflected from the front surface of the crystalline lens, their separation gives the measure of accommodation. The other pair of images is from the cornea. The dark area surrounding these four images is the shadow of the small photographic lens, the rest of the field is fogged by light reflected from the cornea.

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TABLE 1. SUBJECT ATTEMPTING TO LOOK INTO DISTANCE IN DARKNESS

No.	Subject	Age	Horizontal muscle balance (prism dioptres)	P.D. (mm)	Accommodation (dioptres)	Convergence (metre-angles)	Deviation relative to distance of accommodation (degrees)
1	B.S.	27	Ortho.	59	0·9	0·3	2·2
2	B.S.	27	Ortho.	59	0·8	0	3·0
3	B.S.	27	Ortho.	59	0·7	0	2·8
4	B.S.	27	Ortho.	59	1·0	0·3	2·8
5	B.S.	27	Ortho.	59	0·8	0	3·0
6	B.S.	27	Ortho.	59	1·0	0·8	1·0
7	B.S.	27	Ortho.	59	0·4	1·0	1·0
8	C.D.B.	26	3·0 Eso.	66	1·0	2·1	4·0
9	C.D.B.	26	2·0 Eso.	66	1·0	1·75	2·8
10	D.A.C.	30	Ortho.	57	0·6	0·4	0·5
11	D.A.C.	30	Ortho.	57	0·9	0	3·0
12	D.A.C.	30	1·0 Exo.	57	0·5	0·5	0
13	D.A.C.	30	0·5 Exo.	57	0·9	0·3	2·1
14	D.S.	32	Ortho.	62	0·6	0	2·2
15	D.S.	32	Ortho.	62	0·8	0·6	1·0
16	D.S.	32	Ortho.	62	1·0	0·4	2·2
17	A.B.L.	28	Ortho.	68	0·3	0·3	0
18	A.B.L.	28	1·0 Exo.	68	0·75	−0·7	5·4
19	A.B.L.	28	1·0 Exo.	68	1·0	−0·6	6·3
20	C.B.T.	27	3·5 Eso.	71	1·0	1·5	2·0
21	C.B.T.	27	3·5 Eso.	71	1·25	1·7	2·0
22	C.B.T.	27	3·5 Eso.	71	1·25	1·2	0
23	C.R.Q.	22	Ortho.	65	0	0·1	0
24	C.R.Q.	22	Ortho.	65	0	0·2	1·0
25	C.R.Q.	22	Ortho.	65	0·4	0·9	2·0
26	S.J.E.	25	Ortho.	65	0	0	0
27	C.J.	18	0·5 Exo.	61	1·0	0	3·5
28	C.J.	18	1·0 Eso.	61	1·4	0·7	1·5
29	C.J.	18	Ortho.	61	1·0	0·6	1·6
30	D.S.B.	25	1·5 Exo.	63	1·0	−0·6	5·8
31	D.S.B.	25	1·5 Exo.	63	0·8	−1·0	6·8

TABLE 2. THE STATE OF ACCOMMODATION AND CONVERGENCE IN DARKNESS, SUBJECTS ATTEMPTING TO LOOK AT POSITION OF OWN FINGER HELD AT $\frac{1}{3}$ METRE

No.	Subject	P.D. (mm)	Horizontal muscle balance (prism dioptres)	Accommodation (dioptres)	Convergence (metre-angles)
1	R.H.	67	Ortho.	0·6	1·5
2	B.S.	59	Ortho.	3·0	1·25
3	B.S.	59	Ortho.	1·2	0·2
4	C.J.	51	Ortho.	2·2	1·7
5	C.S.	66	4 Eso.	0·7	1·0
6	C.R.Q.	65	Ortho.	1·4	2·5
7	D.A.C.	57	1·5 Exo.	1·0	0·8
8	P.A.	64	Ortho.	0·2	1·2
9	L.W.	60	1·5 Exo.	0·5	0·4

TABLE 3. ACCOMMODATION AND CONVERGENCE WHEN LEFT EYE FIXATED DISTANT OBJECT AT NEAR-THRESHOLD LUMINANCE

Subject	Accommodation (dioptres)	Convergence (metre-angles)
D.A.C.	0·4	0·5
B.S.	0·8	0·8
C.J.	0·8	0·7
A.B.L.	0·7	0·6
C.R.Q.	0·5	0·4
L.W.	0·7	0·7
P.A.	0·6	0·7

governed by fusion. Because of this the results are of course influenced by the heterophoria. Only orthophoric and exophoric subjects were recorded. In all cases the convergence recorded was the difference between the vergences of the visual axes for monocular fixation of a bright object, and for one with low luminance. The record with fixation of the bright object was made within 2 min of the other, and probably gave a true objective measure of the horizontal muscle balance. Heterophoria was always found to be in the same direction as given by the usual subjective clinical method, but was much larger. A number of esophoric subjects were tested but have not been recorded. It was found in esophoria that convergence tended to be unchanged in low illumination. The esophoria was presumably causing more convergence than would normally accompany the accommodation due to low illumination.

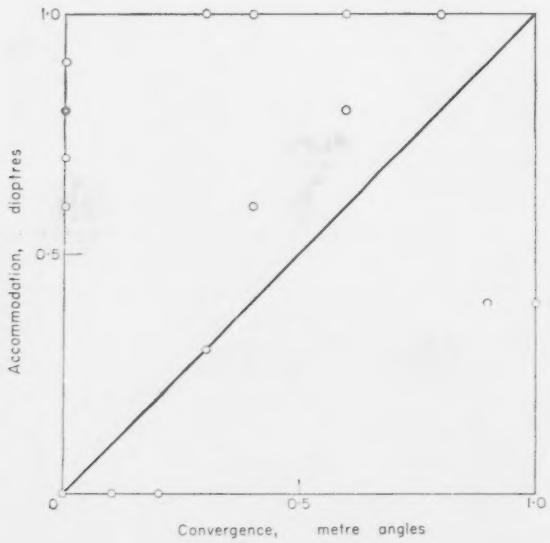

FIG. 4. Accommodation and convergence when subjects attempted to look into distance in darkness: the diagonal line shows equality of accommodation and convergence, the condition in normal vision—Orthophoric subjects.

The results of all the experiments are shown in the graphs (Figs. 4 to 8). Figs. 4, 5 and 6 show the response of accommodation and convergence when subjects attempted to look into distance in darkness. Because there appeared to be some general differences in the results relative to the muscle balance of the subjects, the orthophoric, esophoric and exophoric cases have been plotted separately. The amount of heterophoria, measured by the usual clinical method, is shown against each result. These amounts are given in metre-angles so that they can be compared with the convergence which the subjects exercised in the experiment.

It is seen that in seventeen results from orthophoric subjects (Fig. 4) accommodation equalled convergence in only two cases, one at zero and the other at 0·3, and in only seven

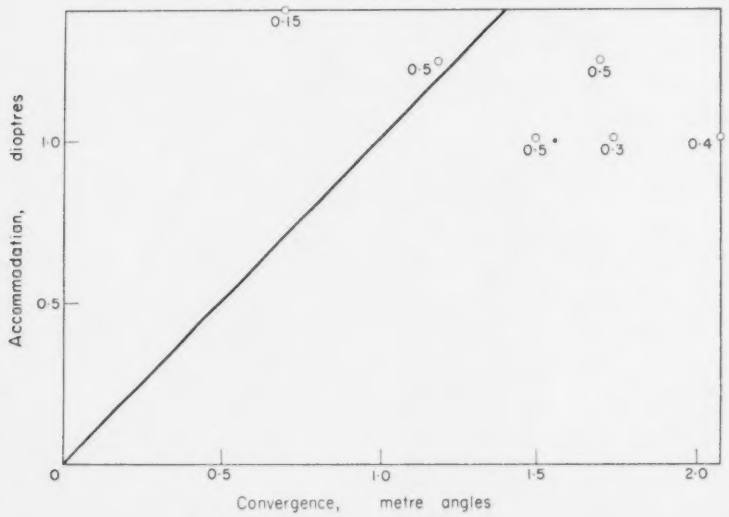

FIG. 5. Accommodation and convergence when subjects attempted to look into distance in darkness—Esophoric subjects: the figures against the points show the esophoria in metre-angles.

were the two functions approximately equal. Two results showed convergence in excess of accommodation, with convergence of approximately 1 metre-angle while accommodation was only 0·4 dioptre. But overall there was a distinct excess of accommodation above convergence. This occurred in twelve results, in five of which accommodation was between 0·6 and 0·9 dioptres while convergence was zero.

In five out of the six esophoric cases (Fig. 5), the convergence was high, as would be expected. The accommodation was also high; in no case less than 1 dioptre. The two functions were equal in one case, but in four convergence was the greater.

The seven results obtained from exophoric subjects (Fig. 6) showed the greatest difference between accommodation and convergence. In one of these there was equality, but in all the other cases accommodation greatly exceeded convergence; one result showed 1 dioptre of accommodation and zero convergence, and four showed accommodation between 0·75 and 1 dioptre, while the eyes were diverging.

DISCUSSION

These experiments have shown that in darkness the convergence of the eyes, like the accommodation, is active by an amount which varies from time to time. As with accommodation, mental effort to control convergence within moderate limits is ineffective. If instead of a complete absence of retinal stimulation, the luminance of the visual field is reduced to near threshold, and fixation of a distant object is maintained, involuntary accommodation still occurs. Tests which are made during monocular fixation of very weakly

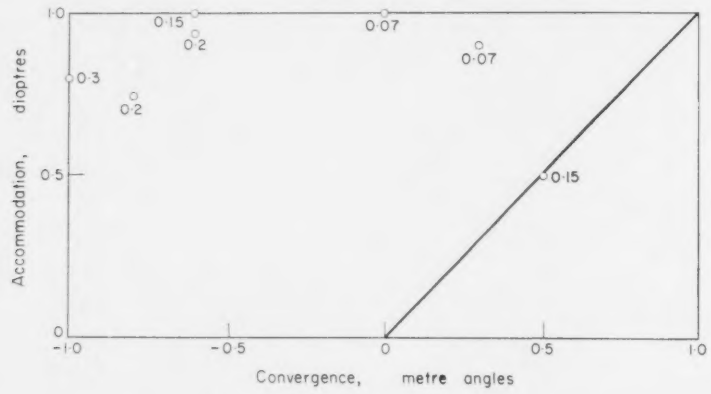

FIG. 6. Accommodation and convergence when subjects attempted to look into distance in darkness—Exophoric subjects: the figures against the points show the exophoria in metre-angles.

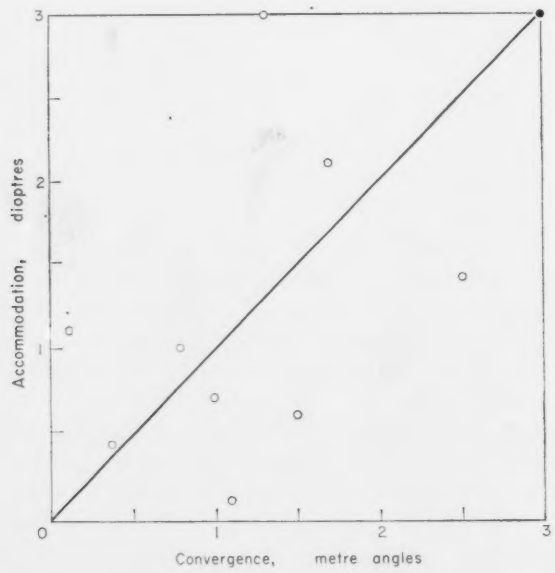

FIG. 7. Accommodation and convergence when subjects attempted to look at position of their own finger held at $\frac{1}{3}$ m in darkness. The solid circle shows the normal condition of accommodation and convergence in vision at $\frac{1}{3}$ m.

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illuminated objects show that under these conditions the eyes also converge to a distance approximately equal to the accommodation distance. This maintenance of the synergic link between accommodation and convergence in the presence of night myopia was shown by the subjective experiments of IVANOFF and BOURDY (1954) and is confirmed by the present objective measurements (Table 3, Fig. 8). The loss of definition in vision in low illumination, due largely to accommodation, is a common experience and gave rise to the early investigation of night myopia, but if the eyes also converge under these conditions we should expect to have diplopia for distant objects. In the present results the deviation of the eyes from parallel is as much as 2°, which would produce noticeable diplopia. This does not appear to have been reported as a characteristic of night vision and could not be detected by the subjects of the present experiments.

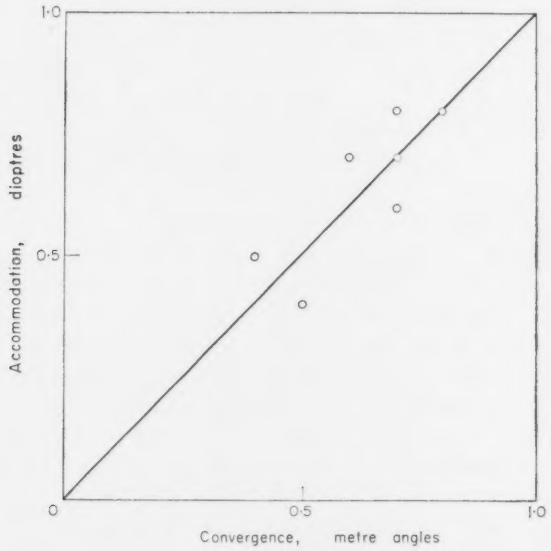

FIG. 8. Accommodation and convergence when left eye fixated distant object at near-threshold luminance, right eye unstimulated.

It appears therefore that in low illumination when accommodation occurs, the eyes do not actually converge if there is binocular vision. The results of the tests with monocular fixation show that latent convergence is present, but in binocular vision, deviation of the eyes is prevented by fusion. This latent convergence is clearly shown subjectively with an instrument of the haploscope or synoptophore type. Such an instrument arranged to measure heterophoria with well-illuminated non-fusible objects is adjusted so that the objects for the right and left eyes are seen in coincidence. If then the apparent luminance of the objects is reduced to near threshold by means of neutral filters placed before the eyes, the objects appear to move in a temporal direction, indicating that the eyes have converged. The movement generally takes two or three seconds to complete. When the filters are removed the objects appear to move back to their original position of coincidence. This

movement is slower and takes about six to eight seconds. In the case of the author who is an absolute presbyope, and therefore shows no accommodation in low illumination, this convergence movement when fusion is prevented is quite marked. Probably in this case the innervation to both accommodation and convergence is present as in young subjects, but due to sclerosis of the lens there is no physical accommodation.

The purpose of the activity of accommodation and convergence in the absence of retinal images is not very clear, especially as the two functions appear from these results to be quite dissociated. We may speculate that in darkness, and also when the visual field is empty of definite stimuli, although illuminated, the eyes are always searching for a stimulus. This could be a defensive precaution. The necessary roving adjustments could apply to both accommodation and the direction of the eyes. It was found by OTERO, PLAZA and SALAVERRI (1949) that a 50 per cent decrease in the absolute threshold for small stimuli occurred when nocturnal myopia was compensated by the use of suitable negative lenses, and they concluded that this was because more light was concentrated into the retinal image. In the same way the eye accommodating in darkness will be better adapted to respond to the divergent light from near objects. Under these conditions accommodation varies in amount from zero to about 1·3 dioptres; CAMPBELL (1953) found a maximum of 1·3, and the highest in the present series of results is 1·4 dioptres. This would cover the range from distance to 30 in, or about arm's length, which may be significant if vision is to serve as a warning of obstacles.

We may wonder then why convergence is not coupled to accommodation, as it is under conditions of normal lighting, so that as soon as a stimulus is sighted it is seen with binocular vision. But that would reduce the efficiency of the visual mechanism in searching. There are advantages in two eyes scanning independently, but linked to a fusion control, which can ensure single perception as soon as a stimulus is found. Although for the detection of a weak stimulus the correct adjustment of accommodation is the most efficient, it may not be the best condition of convergence. If the visual axes are converged to the distance to which the eyes are accommodating, the binocular zone of greatest retinal sensitivity, relative to a stimulus at that distance, will be approximately equal to the maximum sensitivity zone of a single eye. If, however, the eyes are dissociated so that they do not converge for that distance the effective zone of maximum sensitivity will be extended, and also there will be less chance of the image falling upon the relatively insensitive fovea in both eyes.

If this interpretation of the results is correct, the changes in the angle between the eyes recorded in these experiments are not an activity of the convergence mechanism as such, but evidence of dissociated scanning movements. This means that in the absence of retinal images Hering's theory of conjugation of innervation to extraocular muscles does not apply, at least for horizontal movements. No deviations in the vertical direction were recorded, but there are probably physiological restrictions on such movements. Also the limitation of movement of one eye, which was necessary in these experiments, may have imposed restrictions, and deviations may well be greater when we are peering into darkness under normal conditions than were found in these experiments.

The graphs of results from heterophoric subjects (Figs. 5 and 6) show a connexion between the state of convergence in darkness and the type of heterophoria. Thus esophoric subjects, i.e. those whose eyes tend to converge when fusion is prevented, showed relatively high convergence in darkness. Similarly, exophoric subjects exhibited low convergence or actual divergence when attempting to look into distance in darkness. The vergences recorded in these experiments were much greater than the heterophorias which were measured by the

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clinical method. A point of particular interest is that the accommodative state in darkness is little affected by the increase or decrease of convergence related to heterophoria. Although the greatest amounts of accommodation were found in esophoria, they were not in proportion to the increased convergence. Accommodation was also still very active in exophoria when the eyes were diverging, and although there were fewer results, it was just as high as in orthophoria. The greater spread in the ratio of convergence to accommodation which is seen in the results from orthophoric subjects, may be because more of these were tested or because we obtain a truer picture of the variations when convergence is not influenced by muscle imbalance.

It has been shown (FINCHAM, 1951) that during vision, changes in accommodation are induced by changes in convergence, in fact if the light vergence stimulus to accommodation is prevented, accommodation is completely controlled by convergence. If the eyes are made to diverge by means of prisms or a stereoscope, accommodation is relaxed. The present experiments have shown that in the absence of retinal images this effect of convergence upon accommodation does not exist, the close link between the two functions no longer applies.

Heterophoria is the condition in which the visual axes deviate from the point to which the eyes are accommodated when fusion is prevented. A subject is said to be orthophoric for distance when, with any error of refraction corrected and accommodation relaxed, the visual axes are found to be parallel when fusion is prevented. It is necessary to relate the muscle balance to the state of accommodation in this way because, during vision, accommodation and convergence influence one another, and the behaviour of one function cannot be studied unless the state of the other is known. As we have seen, accommodation and convergence do not influence one another in darkness, but there is, nevertheless, under these conditions, some agreement between the vergence of the eyes and the heterophoria measured during vision with accommodation relaxed. This persistence of the condition of vergence, although vision is not stimulated, is some indication that heterophoria is anatomical rather than functional in origin.

The results in Table 2, Fig. 7, show that the brain is unable to use the information given by the proprioceptor nerves of the hand and arm to direct the eyes and adjust accommodation. The controls for these adjustments in both near and distant vision must depend upon the presence of retinal images. How far the innervation is voluntary may depend upon the brightness of the images and the amount of adjustment to be made, but without images we are unable mentally to control either convergence or accommodation. As soon as images are received by the retinae a complex system, partly reflex, for directing and focusing the eyes comes into operation. This entails, with images of normal brightness, fixation and binocular fusion, and accommodation controlled by reflex from the convergence innervation and the vergence of the light at the retina.

Acknowledgements—The author wishes to thank all those who acted as subjects in these experiments. Thanks are also due to DR. R. A. WEALE and DR. F. W. CAMPBELL for helpful conferences.

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Vision Res. Vol. 1, pp. 441–443. Pergamon Press 1962. Printed in Great Britain.

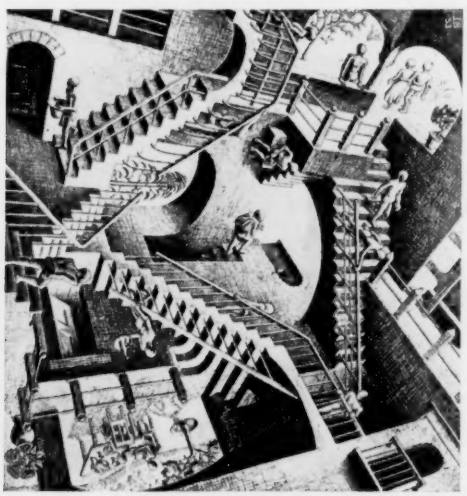
EDITORS' NOTES

PERSPECTIVE was used correctly by the artist-architect Leon Battista Alberti (1404–1472) many years before the mathematician Gerard Desargues (1593–1662) formalized the mathematical relationships in his famous theorem. Surely it behoves those of us interested in visual science to remain in particularly close touch with the profound visual imagination of the artist because it so often exceeds our own.

In this connection it is of interest to note the recent work of the Dutch artist, M. C. Escher (Catalogue No. 118, Stedelizk Museum, Amsterdam, 1954; *The Graphic Works of* . . . Duell, Sloan and Pierce, New York, 1961). With the kind permission of the artist, we reproduce here one of his most provocative graphics.

Mr. Escher's use of multiple perspective is an extraordinarily vivid demonstration of the power of monocular cues for the perception of depth. More than this, he has created a fundamentally insoluble perceptual and intellectual paradox.

T. S.



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International Society for Clinical Electroretinography,
"Symposium on Standardization of the clinical ERG",
Stockholm, Sweden,
1–3 June 1961.

REPORT

The general impression was that of a well-organized meeting, held in a friendly and informal atmosphere. This made it easy to achieve the important common objectives. Forty-one out of ISCERG's 160 members were present, coming from fourteen countries.

The following aspects of the problem were presented:

Stimulus light source:

"Advantages and disadvantages of the use of gas discharge tubes as a light source in clinical electroretinography", by van der Tweel (Netherlands), with Lucia Ronchi (Italy) as discussant.

Contact glasses:

"A comparative study of the single flash ERG using different types of contact glasses", by Sundmark (Sweden) and Burian (U.S.A.), with Henkes (Netherlands) as discussant. Echte and Pabst (W. Germany) presented a new type of contact glass supplied with a lens of +50 D or more, allowing for wide-angle stimulation of the retina. The indifferent electrode is mounted at the outside of the scleral part of the glass.

Pupil size:

"The influence of pupil size in the ERG", by Karpe (Sweden) and Wulfing (Sweden), with François (Belgium) as discussant.

Size of retinal field stimulated:

"A comparative study of the ERG after stimulation with a large field of low intensity vs. stimulation with a small field of high intensity", by De Rouck (Belgium), with Best (W. Germany) as discussant.

Procedure:

"The role of pre-adaptation to light in clinical electroretinography", by Elisabeth Schömer (E. Germany), with Bornschein (Austria) as discussant.
(A report covering "Procedure, Measurement, and Terminology", by Burian and Arnott (U.S.A.), could not be discussed as neither author was able to attend the meeting.)

Conclusions reached will be clarified and presented to the membership in the form of recommendations to be published in the *Newsletter* of the Society.

The last day of the meeting was devoted to papers at large covering the broad field of electrophysiology and pathology of the retina:

YONEMURA (Japan): On the oscillatory potential of the ERG.

SCHMÖGER (E. Germany): Problems of adaptation during ERG-registration.

BORNSCHEIN (Austria): The response of the human eye to red stimuli with different temporal gradients of luminance.

HENKES and VAN BALEN (Netherlands): Periodical integration of retinal responses following repetitive light stimuli—a method for the demonstration of minor changes in retinal activity.

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BAUMANN, DETTMAR, HANITZSCH, HASCHKE and SICKEL (E. Germany): Effects of light and non-optical influences on the isolated retina as reflected on the ERG.

PABST and ECHTE (W. Germany): Increment threshold of achromatic children as measured by the ERG.

PEREGRIN and SVERAK (Czechoslovakia): Some physiological aspects of ERG-glare test.

KARPE and GERMANIS (Sweden): The prognostic value of the ERG in thrombosis of the retinal vein.

WIRTH and APOLLONIO (Italy): High-intensity ERG in retinitis pigmentosa.

RUBINO and PONTE (Italy): The role of ERG in diagnosis and prognosis of the retinitis pigmentosa.

PONTE (Italy): Electroretinography in solar macular injury.

SCHMIDT and MÜLLER-LIMMROTH (W. Germany): Electroretinographic examinations following the application of Chloroquine.

RENDAHL (Sweden): ERG and prognosis in retinal detachment.

RONCHI and ERCOLES (Italy): Training and ERG responses.

A great deal of discussion took place following most of the papers. The standardization reports, the discussions of these reports and the general papers will be published in a special issue of *Acta Ophthalmologica*.

Professor Dr. Arndt Kohlrausch, Professor Emeritus of Physiology of the University of Tübingen, was elected an honorary member of the Society.

H. E. HENKES

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International Commission for Optics,
"Image Formation and Vision",
Munich, Germany,
19–26 August 1962.

According to previous meetings, which are held every four years, approximately 700–800 scientists from all over the world will probably participate in the Munich Congress. The following subjects are scheduled:

Image formation and vision

1. Photometry of optical instruments and glasses, especially of microscopical objects.
2. Image quality and the role of receptors.
3. The behavior of the visual organs in relation to perception.

H. S.

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